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ERNEST HENRY WILSON

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With portrait

THE sudden death on October 15 of Ernest Henry Wilson, Keeper of the Arnold Arboretum, in an automobile accident, was a great shock to his associates and friends, taking him in the prime of his life from the work he loved so well and in which he was interested with all his heart.

Ernest Henry Wilson was born at Chipping Campden in Gloucestershire, England, on February 15, 1876, the eldest son of Henry and Annie (Curtis) Wilson. After leaving school he entered the nurseries of Messrs. Hewill at Solihull, Warwickshire, and in 1892 was recommended to the Curator of the Birmingham Botanical Gardens as a promising young gardener. He accepted a position in these gardens and notwithstanding the long hours of work he studied at the same time in the Technical School in Birmingham which offered excellent facilities for the study of botany, and did so well that he won the Queen's prize in this subject at the examination held by the Board of Education. In January 1897 he entered the Royal Botanic Garden at Kew where he soon succeeded in winning recognition for his work in the garden as in the lecture room. On the advice of his friends and induced by his love of botany he left Kew and entered in October 1898 the Royal College of Science at South Kensington with the intention of becoming a teacher of botany.

About this time the nursery firm of Veitch & Sons asked the director of Kew Gardens to recommend a suitable man to send to China to collect seeds and living plants. The choice fell on Wilson and he left England in April 1899 for China by the way of Boston and San Francisco. This was his first visit to Boston and to the Arnold Arboretum. One of the chief objects of his journey was the introduction of *Davidia involucrata* and he had instructions to see Dr. A. Henry who was at that time in Szemao, Yunnan, and obtain information where to find this tree which Dr. Henry had seen in Hupeh nearly 20 years before. Arrived at Hongkong he had to sail to Haiphong in Tonkin as the best way to reach Szemao. After much delay and with great difficulties owing to political disturbances[1] Wilson finally succeeded in reaching Szemao. After Dr.

[1] A vivid description of this episode is found in Wilson's Aristocrats of the Garden, pp. 275–294.

Henry had given him the desired information and all possible advice and assistance, he returned to Hongkong and went from there early in 1900 to Shanghai and up the Yangtze River to Ichang. There he found some of Dr. Henry's men who guided him to the place where Dr. Henry had seen the *Davidia* tree, but to Wilson's dismay all he found was the stump of the tree which had been cut down a few years previously. Wilson then decided to collect all the interesting plants of the region he could and in traveling around for this purpose he found in another locality trees of *Davidia* in full bloom, from which he collected in autumn a rich harvest of seed. With Ichang as his headquarters he collected in Hupeh, during 1900 and 1901, seeds and living plants of a great number of new ornamental plants and also a large amount of herbarium material.

In April 1902 he returned to England and on June 8 married Ellen Ganderston of Edgbaston, Warwickshire. Mrs. Wilson, quiet and unassuming, found her highest pleasure in making the happy atmosphere of the home in which he loved to write of his adventures in far away lands. They had one daughter, Muriel Primrose, who, was married last year to Mr. George Slate, a member of the staff of the New York Agricultural Experiment Station at Geneva, N. Y.

He had been so successful in his work that Messrs. Veitch & Sons decided to send him again to China, and in January 1903 he started on a second expedition. He arrived in Shanghai on March 22, and started at once for northern Szechuan. He made Kiatingfu his headquarters and first went to Tachienlu and later north to Sungpan where he found among other things *Meconopsis punicea.* The year 1904 also he spent in the exploration of western Szechuan and returned in March 1905 to England, where he attended for some time to his introductions in the Veitchian nurseries at Coombe Wood and later went as temporary assistant to the Herbarium at Kew to assist in the sorting and identification of his herbarium collections. He had sent in during the expeditions about 2000 numbers of seeds and plants and about 5000 numbers of herbarium specimens of which many proved new to science. In January 1906 he accepted a position as botanical assistant at the Imperial Institute in London.

The success of Wilson as a collector of seeds and living plants and of herbarium specimens attracted the attention of Professor C. S. Sargent and he secured Wilson's services for another exploring expedition to China this time in behalf of the Arnold Arboretum. In December 1906 Wilson came to the Arnold Arboretum and left on the last of the month for China via San Francisco. He arrived in Shanghai on Feb. 4th and proceeded at once to Ichang. He made an excursion in April to the southwest, where at an altitude of 7000 ft. the trees were still bare and snow was lying in the crevices. On this trip he discovered *Pinus Bungeana* wild in Central China. During the rest of the year he explored western Hupeh in different directions with Ichang as the base where he also spent

the winter. In May of 1908 he traveled west and using Kiating as the base, explored western Szechuan in different directions finding the Min valley, Mt. Wa and Mt. Omei particularly interesting and profitable. At the end of the year he left Szechuan and went east again and leaving China towards the end of April 1909 arrived in England on May 15. He stayed in London until September when he returned to the Arnold Arboretum.

As the Conifers in western China did not bear cones in the autumn of 1908 and as it seemed important to secure cones and seeds of these trees, Wilson went to China for the fourth time in April 1910. He traveled by the Trans-Siberian railway via Moscow and Peking and arrived at Ichang by the end of May. As the men who had traveled with him on his former expeditions had been already notified, he was able to start without delay for western Szechuan and reached Chengtu on July 27. At the beginning of August he set out for Sungpan and after having collected there and having made arrangements for digging the bulbs of the Regal Lily in October, he started on his return trip to Chengtu. When following a narrow trail along a steep slope Wilson's party was surprised by a rock slide and Wilson was hit by a rock which broke his right leg in two places below the knee. He was still three days from Chengtu and with his leg temporarily bandaged with splints improvised from the legs of his camera tripod he had to be carried to Chengtu where he was cared for by doctors of the Friends' Presbyterian Mission, but infection had set in and at the end of six weeks as there were no signs of the bones uniting the question of the amputation of the leg was raised. The doctors, however, finally succeeded in staying the infection and after three months Wilson was able to walk on crutches.[1] Soon after he started on his return voyage to America where he arrived in March 1911. After spending a few weeks in a Boston hospital, where he had his right leg, which was nearly an inch shorter reset and fitted with a special boot, he was able to walk freely again. In 1910 the Conifers in western Szechuan had fruited freely and were collected as were the Lily bulbs by Wilson's trained collectors, so that notwithstanding the unfortunate accident the object of the expedition was realized.

During the two Arboretum expeditions Wilson collected about 65,000 specimens representing 4700 numbers and secured 1593 lots of seed and 168 lots of plants and cuttings, also about 850 excellent photographs of plants, general views of vegetation, and of other objects of interest.

From March 1911 to the end of 1913 he remained at the Arnold Arboretum sorting and classifying his collections and preparing jointly with the writer an account of his collections in China edited in three volumes by C. S. Sargent under the title "Plantae Wilsonianae."

In 1914 he went to Japan and spent February and March in southern Japan paying special attention to Cherries; in one garden, where 80

[1] See Wilson, Plant hunting II. 150–153.

garden forms were grown, he collected herbarium material of 63 named forms. From April to June he collected in Central Japan and in July and August in Hondo and Saghalin. In autumn he returned to central Japan and the last two months of the year he spent on the island of Shikoku. After having collected about 2000 numbers with many duplicates, taken about 600 photographs and sent home a large collection of Japanese cherries and seeds he returned to the Arnold Arboretum in January 1915.

From January 1915 to the end of 1916 he assisted again, after having worked and arranged his Japanese collections, in the preparation of the "Plantae Wilsonianae," the last part of which was issued in January 1917.

In January 1917 he started on his sixth voyage to the Far East and explored first in February and March the Liukiu and in April the Bonin Islands. In May he left for Korea and made several excursions with Dr. Nakai, the government botanist of Korea, and during 1917 visited almost all the provinces and also the southern island of Quelpaert and the small Dagelet Island whose flora is closely related to that of Japan. After having spent the last months of the year in the southern provinces he returned in January 1918 to Japan to proceed at once to Formosa where he arrived on January 22; he visited Mt. Arisan where *Taiwania cryptomerioides* the tallest tree of Eastern Asia grows and also ascended Mt. Morrison the highest peak of Formosa (13072 ft.). In April he left the island and returned to Japan where he visited the city of Kurume on Kyushu Island to see a collection of 250 named kinds of Kurume Azaleas; this collection was started by Motozo Sakamoto about 100 years ago and is now in the hands of K. Akashi; the parent stock came from Mt. Kirishima.[1] In June he made a second trip to Korea where he stayed until September 28, when he returned to Japan to visit Formosa once more. About the middle of December he left Formosa and after a short sojourn in Japan returned to the United States arriving in Boston on March 17, 1919. From this last expedition he brought back about 30,000 specimens representing 3268 numbers and 700 photographs, also many seeds and living plants. Some of the most interesting plants he introduced during this expedition are *Taiwania cryptomerioides*, *Pinus luchuensis*, *Juniperus taxifolia* and *Cunninghamia Konishii*.

In April 1919 Wilson was appointed Assistant Director of the Arnold Arboretum and in July 1920 started on a tour to Australia, New Zealand, India and Central and South Africa. He first went to England whence he embarked in September for Australia where he visited the Botanic Gardens at Perth, Adelaide, Melbourne, Sydney and Brisbane and made collecting tours into the native forests. February and March of 1921 he spent in New Zealand and Tasmania, then returned to Australia which country he left in June for Singapore. From Singapore he went to Penang, Rangoon and Calcutta and during August made a tour through the northern and north-western forests, visiting the botanic gardens at

[1] See Wilson, Plant hunting, II. 232–244.

Lucknow, Saharampur, Lahore, Simla and the Forestry College at Dehra Dun. In September he made a tour to Sikkim and Assam and in October went to Bombay and from there to Ceylon and later to the Nilghiri Hills visiting Ootacamund and Coimbatore. On Nov. 4 he sailed from Bombay for Mombasa in East Africa whence he proceeded at once to Nairobe in British East Africa; from there he visited Kenya and the forest where *Juniperus procera* grows. In the beginning of 1922 he went to Portuguese East Africa and thence to Victoria Falls in Rhodesia. On February 2 he reached Pretoria and from there traveled to Durban and Capetown. From Capetown he sailed on April 7 for London in June he paid a visit to Edinburgh and in July made a trip to France. On August 15 he sailed from Liverpool for the United States to take up again his duties as Assistant Director of the Arnold Arboretum. During this last tour he took 522 photographs and collected a large number of herbarium specimens in all the countries he visited. He fully realized the chief object of this tour which was to bring about closer relations between the Arboretum and other botanical institutions all over the world and to establish friendly relations with individuals interested in botany, horticulture and forestry. In April 1927 after the death of the Director, Professor C. S. Sargent, he was appointed Keeper of the Arnold Arboretum.

On October 15, 1930, Dr. and Mrs. Wilson were returning from a visit to their daughter. When near Worcester, Mass., the automobile which Dr. Wilson was driving skidded on a road made slippery by fallen leaves and swerving across the side walk crashed through a wooden fence and dropped over a steep embankment to a field 40 ft. below the level of the road. Mrs. Wilson was dead when extricated and Dr. Wilson died on the way to the hospital without regaining consciousness.

Wilson's chief contribution to horticulture and botany lies in his exploration of China where he spent most of his time between 1899 and 1911. His long sojourn in this country and his familiarity with it earned for him the epithet "Chinese" Wilson. He made four journeys to China and in all six to the Far East, the last two to the different countries of the Japanese Empire. He was a born plant collector; endowed with a strong physique, robust health, indomitable will power and a deep love of plants he succeeded in collecting and introducing into cultivation a greater number of plants than any other collector. He knew how to handle his men and never had any serious trouble in all his expeditions in the Far East. He introduced more than a thousand species previously unknown to cultivation and collected about 16,000 numbers of herbarium specimens, with numerous duplicates, so that now his specimens are found in all important herbaria throughout the world and his plants have spread to all the gardens of temperate and subtropical regions. It is not feasible to enumerate here all his introductions and only a few of the more important can be mentioned, as: *Abelia Schumannii* Rehd., *Abies Fargesii* Franch., *Acer Davidii* Franch., *Actinidia chinensis* Planch.,

Aesculus Wilsonii Rehd., *Ampelopsis megalophylla* Diels & Gilg, *Berberis Sargentiana* Schneid., *B. triacanthophora* Fedde, *Buddleia Davidii* var. *magnifica* Rehd. & Wils., *Buxus microphylla* var. *koreana* Rehd. & Wils., *Catalpa Fargesii* Bur., *Celastrus angulata* Maxim., *Cercis racemosa* Oliv., *Citrus ichangensis* Swingle, *Cladrastis Wilsonii* Takeda, *Clematis montana* var. *rubens* Ktze., *Corylopsis Veitchiana* Bean, *Cotoneaster apiculata* Rehd. & Wils., *Cunninghamia Konishii* Hay., *Deutzia longifolia* var. *Veitchii* Rehd., *Dipteronia sinensis* Oliv., *Evonymus Aquifolium* Loes. & Rehd., *Forsythia ovata* Nakai, *Fagus lucida* Rehd. & Wils., *Fortunearia sinensis* Rehd. & Wils., *Gaultheria Veitchiana* Craib, *Hamamelis mollis* Oliv., *Hydrangea Sargentiana* Rehd., *Ilex Pernyi* Franch., *Jasminum primulinum* Hemsl., *Kolkwitzia amabilis* Graebn., *Liquidambar formosana* Hance, *Liriodendron chinense* Sarg., *Lonicera tragophylla* Hemsl., *Magnolia Delavayi* Franch., *Malus theifera* Rehd., *Neillia sinensis* Oliv., *Photinia Davidsoniae* Rehd. & Wils., *Picea asperata* Mast., *Pieris taiwanensis* Hay., *Populus lasiocarpa* Oliv., *Prunus Dielsiana* Koehne and many varieties of *P. serrulata* Lindl. and *P. Lannesiana* Carr., *Pyrus Calleryana* Dcne., *Rubus lasiostylus* Focke, *Rosa Moyesii* Hemsl. & Wils., *Salix magnifica* Hemsl., *Sargentodoxa cuneata* Rehd. & Wils., *Schizophragma integrifolium* Oliv., *Sinofranchetia chinensis* Hemsl., *Sinowilsonia Henryi* Hemsl., *Sorbaria arborea* Schneid., *Sorbus Sargentiana* Koehne, *Spiraea Veitchii* Hemsl., *Staphylea holocarpa* Hemsl., *Stewartia koreana* Nakai, *Styrax Wilsonii* Rehd., *Sycopsis sinensis* Oliv., *Syringa reflexa* Schneid., *Taiwania cryptomerioides* Hay., *Thea cuspidata* Kochs, *Tilia Oliveri* Szysz., *Tsuga yunnanensis* Mast., *Vaccinium praestans* Lamb., *Viburnum rhytidophyllum* Hemsl., *Vitis Davidii* Foëx, *Aconitum Wilsoni* Stapf, *Astilbe Davidii* Henry, *Corydalis thalictrifolia* Franch., *Lilium regale* Wils., *Meconopsis integrifolia* Franch., *Primula Veitchii* Duthie, *Rodgersia aesculifolia* Batal., *Senecio tanguticus* Maxim., *Thalictrum dipterocarpum* Franch., *Rehmannia angulata* Hemsl., and others.

During his travels in different parts of the world Wilson paid much attention to forest conditions and published valuable contributions and suggestions relating to the forest problems of several countries, as Korea (A summary report forestry and afforestation of Chosen. 1919), East Africa (Indigenous forest trees of Kenya. 1922), South Africa and Australia (Northern trees in southern lands. 1923). He also rendered a great service to silviculture through the introduction of important forest trees into cultivation.

In his position as Keeper of the Arnold Arboretum he carried on the work of Professor Sargent and succeeded well in maintaining its steady progress and development. Besides this work he took an active interest in the Massachusetts Horticultural Society of which he was trustee and member of several important committees, and was advisory editor of the Society's publication "Horticulture." He also was much sought for as a lecturer by horticultural societies in different parts of the country

and particularly he liked to lecture on the Arnold Arboretum, the subject closest to his heart. Notwithstanding all these activities he found time for literary work. He was a frequent contributor to horticultural and botanical periodicals and published a number of important horticultural and botanical books; he wrote of his experiences in China in "A Naturalist in Western China," "Plant Hunting" and "China, Mother of Gardens"; he dealt with ornamental plants, chiefly trees and shrubs, in "Aristocrats of the Garden," "More Aristocrats of the Garden," "Aristocrats of the Trees," and "America's Greatest Garden" which is a description of the Arnold Arboretum. More strictly botanical are "Cherries of Japan," "The Conifers and Taxads of Japan," "A monograph of Azaleas (with A. Rehder)" and "The Lilies of Eastern Asia." Wilson's books are well written. In his botanical publications he covers his ground completely with painstaking accuracy, knowing the plants he is dealing with not only from the study of ample herbarium material but also as they grow in their native habitat; in his more popular books he writes in a vivid and entertaining style imparting his masterly knowledge of the plants in a way that keeps the interest of the reader alive from cover to cover. Not the least valuable part of his books are the reproductions of the excellent photographs he took in all parts of the world.

Many honors were bestowed upon Wilson. On November 6, 1906 he received the Veitchian medal in recognition of his services in horticulture and in 1913 the Victoria medal of honor in horticulture. He also received the Geoffroy St. Hilaire Gold Medal, the George Robert White Medal, the Medal of the Horticultural Society of New York and the Centennial Gold Medal of the Massachusetts Horticultural Society. In 1916 the honorary degree of A.M. was conferred on him by Harvard University and in 1930 the honorary degree of Sc.D. by Trinity College of Hartford, Conn. He was elected fellow of the American Academy of Arts and Sciences, was an honorary member of the Rhododendron Society, the American Horticultural Society and also was a member of other scientific and horticultural societies. In recognition of his services to Chinese botany a new genus of Hamamelidaceae from China, *Sinowilsonia*, was named in his honor. Besides this, about 60 species and varieties of Chinese plants bear his name of which some may be cited here: *Aconitum Wilsonii* Stapf, *Aesculus Wilsonii* Rehd., *Aralia Wilsonii* Harms, *Cladrastis Wilsonii* Takeda, *Corydalis Wilsonii* N. E. Br., *Daphne Wilsonii* Rehd., *Deutzia Wilsonii* Rehd., *Evonymus Wilsonii* Sprague, *Ilex Wilsonii* Loes., *Iris Wilsonii* C. H. Wright, *Magnolia Wilsonii* Rehd., *Populus Wilsonii* Schneid., *Rubus Wilsonii* Duthie, *Salix Wilsonii* Schneid., *Sophora Wilsonii* Craib, *Sorbus Wilsoniana* Koehne, *Spiraea Wilsonii* Rehd., *Styrax Wilsonii* Rehd., *Ulmus Wilsoniana* Schneid., *Viburnum Wilsonii* Rehd.

Although Wilson was taken from us in the full vigor of his life, he had

already accomplished so much that his memory cannot die with us who knew him both personally and as a friend. His name will live through generations to come in the new plants he discovered many of them commemorating his name and in the plants he brought from foreign lands to enrich and embellish our gardens.

LIST OF PUBLICATIONS OF ERNEST HENRY WILSON

Western China, a field for the sportsman. (In Field 1905, cvi, 109.)

Rubus innominatus. [London. 1905.]
"From the *Gard. chron.*," 1905, 3d ser., xxxviii, 290–291.

Leaves from my Chinese note-book. (In Gardeners' chronicle, ser. 3, 1905–06, xxxvii–xxxix.)

Vegetables. Illustr. (In Freeman, W. G., and Chandler, S. E. The world's commercial products, 1907, pp. 254–263.)

Fruits. Illustr. (Ibid, 1907, pp. 263–278.)

[Arnold arboretum expedition to China, 1907–1909; a series of 720 photographs.]

Gardeners' chronicle (contributions in). 1907–24, ser. 3, xli–lxxv. 30 articles.

Chinese Rhodendrons. [In collaboration with W. B. Hemsley.] (Kew bulletin of miscellaneous information, 1910, pp. 101–120.)

Plant novelties from China. (in Horticulture, 1910, xi, 5, 37, 69, 105, 145, 181, 221, 257, 293, 329, 367, 433, 473.)

Field notes relating to plants collected on the Arnold arboretum second expedition to Western China, 1910. London, *etc.* [1911].

[Arnold arboretum second expedition to China, 1910–1911; a series of 384 photographs.]

The kingdom of flowers. Illustr. (in National geographic magazine, 1911, xxii, 1003–1035.)

Sargent, C. S., editor. Plantae Wilsonianae (contributions in). 1911–17. 12 articles by E. H. Wilson; 47 articles in collaboration with Alfred Rehder.

Vegetation of western China. Introduction by C. S. Sargent. London. 1912. (Arnold arboretum. Publications, 2.)
An index to accompany a selection of 500 photographs from his "Arnold arboretum expedition to China, 1907–1909."

A naturalist in western China; being some account of eleven years' travel. With introduction by C. S. Sargent. 2 vol. London, Methuen & Co. [1913.] Plates.

The same. 2 vol. New York, Doubleday, Page & Co. 1913. Plates.

The "wood-oil" trees of China and Japan. [London. 1913.]
Bulletin of the Imperial institute, 1913, xi, 441–461.

[The Arnold arboretum expedition to Japan, 1914; a series of 619 photographs.]

The family tree of the modern rose. Done into graphic form by F. A. Wilson. [Boston.] 1915. Chart 24⅞ x 18½ in.

The Cherries of Japan. Cambridge, University Press. 1916. (Arnold arboretum. Publications, 7.)

The Conifers and Taxads of Japan. Cambridge, University Press. 1916. (Arnold arboretum. Publications, 8.)

A century of certified plants introduced from China. (In Journal of the Royal horticultural society, 1916, xlii, 35.)

The history and botanical relationships of the modern rose. [In collaboration with F. A. Wilson.] N. P. cop. 1916. Chart 32⅝ x 25⅛ in.

The American Rose annual (contributions in).
[i.] 1916. Some new Roses introduced by the Arnold arboretum during the past decade, pp. 37–41.
[viii.] 1923. Roses in Australia, pp. 118–120.
[ix.] 1924. What Roses does America need? pp. 23–25.

Aristocrats of the garden. Garden City; New York, Doubleday, Page & Co. 1917. Plates.

The same. [2d ed.] Boston, The Stratford Company. 1926. Plates.
This edition has an entirely new set of plates.

The vegetation of Korea. [Seoul. 1918.]
Reprinted from the *Transactions of the Korea branch of the Royal Asiatic society,* 1918, ix, 1–16.

A summary report on the forests, forest trees, and afforestation in Chosen (Korea). [Edinburgh. 1919.]
Reprinted from *Transactions of the Royal Scottish arboricultural society,* 1919, xxxiii, 44–51.

Work of Arnold arboretum. Broadside. Illustr.
Reprinted from *Christian science monitor,* June 2–4, 1919.

The romance of our trees. Garden City; New York, Doubleday, Page & Company. 1920. Plates.
Enlarged from articles in *Garden magazine,* 1919–20.

Kurume Azaleas. (In Bulletin of the Massachusetts horticultural society, 1920, no. 3.)

Journal of the Arnold arboretum (contributions in).
i. 1920 ['19–20]. A phytogeographical sketch of the ligneous flora of Korea, pp. 32–43; The Bonin Islands and their ligneous vegetation, pp. 97–115; New woody plants from the Bonin Islands [in collaboration with Alfred Rehder], pp. 115–121; The Liukiu Islands and their ligneous vegetation, pp. 171–186; Four new Conifers from Korea, pp. 186–190; Camphor, Cinnamomum camphora Nees & Ebermaier, pp. 239–242.
ii. 1922 ['20–22]. A phytogeographical sketch of the ligneous flora of Formosa, pp. 25–41; The "Indian Azaleas" at Magnolia gardens, pp. 159–160; Notes from Australasia, i, ii, pp. 160–163, 232–236.
iii. 1922. Notes from Australasia, iii, pp. 51–55.
iv. 1923. The Rhododendrons of northeastern Asia exclusive of those belonging to the subgenus Anthodendron, pp. 33–56; Northern trees in southern lands, pp. 61–90; The Hortensias, Hydrangea macrophylla DC. and Hydrangea serrata DC., pp. 233–246.
v. 1924. The Rhododendrons of Hupeh, pp. 84–107; A new species of Reevesia, pp. 233–235.
vi. 1925. The Rhododendrons of eastern China, the Bonin and Liukiu Islands and of Formosa, pp. 156–186; Rhododendron chrysocalyx *Lév. & Vaniot,* pp. 200–201.
vii. 1926. The Taxads and Conifers of Yunnan, pp. 37–68; Thuja orientalis Linnaeus, pp. 71–74; Gymnospermae [of New Caledonia], pp. 76–85.
viii. 1927. Juniperus procera Hochst., pp. 1–2; An enumeration of the ligneous plants of Anhwei, by Alfred Rehder and Ernest H. Wilson, pp. 150–199; 238–240.
ix. 1928. Enumeration of the ligneous plants collected by J. F. Rock on the Arnold Arboretum expedition to northwestern China and northeastern Tibet, by Alfred Rehder and Ernest H. Wilson, pp. 4–27; 37–125; Podocarpus falcata R. Br., pp. 143–144.
x. 1929. Widdringtonia juniperoides, pp. 1–2.
xi. 1930. Thuya orientalis and Juniperus chinensis, pp. 135–136.

A monograph of Azaleas [in collaboration with A. Rehder]. Cambridge, University Press. 1921 (Arnold arboretum. Publications, 9)

The Azaleas of the Old World; by E. H. Wilson.—The Azaleas of North America; by Alfred Rehder.

Indigenous forest trees of Kenya. 2 pt. (in The Farmers journal of East Africa 1922, iv, no. 8, pp. 17–20; no. 10, pp. 17–20.)

Rhododendron society notes (contributions in).
ii. 1922–24. The Rhododendrons of northeastern Asia, pp. 93–106; The Rhododendrons of Hupeh, Central China, pp. 160–174; The Rhododendrons of the Bonin and Liukiu Islands and of Formosa, pp. 228–240.
iii. 1925 ['26]. The Rhododendrons of eastern China, pp. 18–28.

Acacias. (In Bulletin of the Massachusetts horticultural society, 1923, no. 11.)

Autumn landscapes.

Christian science monitor, Oct. 8, 1923.

Garden magazine (contributions in). Illustr.
xxxvi–xxxviii. 1923–24. Travel tales of a plant collector, xxxvi, 264–268, 309–311; xxxvii, 35–38, 127–130, 185–189, 247–252, 326–330, 384–387; xxxviii, 35–39, 101–105; Indian Azaleas at Magnolia, p. 159; Travel tales of a plant collector, pp. 170–173, 285–287, 355–359.
xxxix. 1924. Where Orchids are at home, pp. 215–219.
30 shorter articles contributed to vol. xix–xxxii, 1914–1921.

Northern trees in southern lands. [Lancaster, Pa., 1923.]

"Reprinted from *Journal of the Arnold arboretum,*" 1923, iv, 61–90.

The same. New issue. 1929.

Country life (contributions in). Illustr.
liii. 1923. Oriental Cherries, pp. 511–514.
liv. 1923. Oriental Crabapples, pp. 9–12; Hawthorns, pp. 681–683.
lv. 1924. American Crabapples, pp. 26–28; The Magnolias, 2 pts., pp. 214–216, 252–253.
lvi. 1924. The modern Rose, 2 pt., pp. 648–650, 679–681; Wild Roses, pp. 848–850.
lvii. 1925. Hardy Azaleas, 2 pts., pp. 339–340, 444–445; Viburnums, pt. 1, pp. 1038–1040.
lviii. 1925. Viburnums, pt. 2, pp. 25–27.

Horticulture (contributions in), 1923–1930, n. s. I–VIII. 99 articles. Illustr.

Harvard's tree museum.

Museum work, 1924, vi, 147–152.

Garden (contributions in), 1924–1926, lxxxviii–xc. 26 articles.

House and garden (contributions in), 1924–1930. Illustr.
xlv. 1924. The royalty of spring, no. 3, pp. 61, 62, 63, 116, 118; Early flowering trees and shrubs, no. 4, pp. 62, 63, 114, 118, 122; Hardy climbers for the garden, no. 5, pp. 70, 71, 120, 122, 124; Wild Roses for the garden, no. 6, pp. 66, 67, 130, 132, 134.
xlvi. 1924. The brilliant gaiety of Azaleas, no. 1, pp. 56, 57, 100, 102, 104; The best hardy Conifers, no. 2, pp. 50, 51, 102, 104, 106, 108; Hawthorns for ornamental planting, no. 3, pp. 70, 71, 124, 126, 130, 132; Green carpets for various grounds, no. 4, pp. 66, 67, 106, 108, 110; Mid-season flowering trees and shrubs, no. 5, pp. 64, 65, 138, 140, 142; Fruiting trees and shrubs, no. 6, pp. 60, 61, 114, 120, 122.
xlvii. 1925. The beauty of the Barberries, no. 1, pp. 76, 77, 110, 114, 116; Winter beauty in the woody plants, no. 2, pp. 80, 81, 106, 108, 110, 114; The Cherries of Japan, no. 3, pp. 92, 93, 114, 116, 122; The Dogwoods and their great variety, no. 4, pp. 78, 79, 100, 102, 104; Honeysuckles in bush and vine, no. 5, pp. 90, 91, 114, 116; The glory of the Lilies, no. 6, pp. 66, 67, 116, 118, 124.

xlviii. 1925. The excellent family of Viburnums, no. 1, pp. 66, 67, 108, 110, 114, 116; The architecture of trees, no. 2, pp. 72, 73, 74, 75, 108, 110, 112; The family of Evonymus, no. 3, pp. 90, 91, 148, 154; Good bulbs from South Africa, no. 4, pp. 72, 73, 136, 138, 140; From Australia come Acacias, no. 5, pp. 92, 93, 120, 122; Curious fruits from many plants, no. 6, pp. 66, 67, 120, 122, 124.

xlix. 1926. Pecans and other Nut trees, no. 1, pp. 74, 75, 118, 122; Some Yews and low-growing Conifers, no. 2, pp. 82, 83, 150, 154; The best street trees for town betterment, no. 3, pp. 112, 182, 186, 188; Twelve best shrubs for ten regions, no. 3, pp. 101, 166; The coming of Kurume Azaleas, no. 4, pp. 112–113, 142, 146, 148; Spring beauty in the garden, no. 5, pp. 116, 117, 150, 154, 156, 170.

51 shorter articles contributed to vol. L–LVIII, July 1926–1930.

America's greatest garden. Boston, The Stratford Company. 1925. Plates.

The same. [2d issue.] Boston, The Stratford Company. 1925. Plates.

The same. Autographed de luxe ed. Boston, The Stratford Company. 1925. Plates.

The same. 3d ed. Boston, The Stratford Company. 1926. Plates.

The Lilies of eastern Asia. London, Dulau & Co. 1925. Plates.

Among the head-hunters of Formosa. (In The Country gentleman, 1925, xc, no. 7, pp. 7, 34.)

New plants from China. (In American forests and forest life, 1925, xxxi, 85–86, 91.) Illustr.

Price of the Regal Lily. (In The Country gentleman, 1925, xc, no. 36, pp. 11, 145.)

Wildrosen (in Gartenschönheit, 1925, vi, 106–109.)

Azaleas in the Arnold arboretum. (In Rhododendron society notes, 1926, iii, 73–76.)

Plant hunting. 2 vol. The Stratford Company, Boston, 1927. Plates.

Charles Sprague Sargent. (In Harvard graduates' magazine, 1927, xxxv, 605–615.)

Identification of the rhododendrons collected by J. F. Rock on the Arnold Arboretum expedition to northwestern China, 1924–27. (In Rhododendron society notes, 1927, iii, 160.)

Arnold Arboretum Bulletin of Popular information, 1927–1930; 3d ser., vol. 1–3.

More Aristocrats of the garden. The Stratford Company, Boston, 1928. Plates.

Plant crabapples for beauty in flower and fruit. (In Garden club of America Bulletin, 1928, no. 23, pp. 14–17.)

Garden cinderellas by Helen Morgenthau Fox. Foreword, pp. vii–ix, 1928.

Korean plants in gardens. (In New flora and silva, 1928, i, 9–21.) Illustr.

History and distribution of the Lilac. (Chapter in Susan D. McKelvey's "The Lilac," pp. 1–6. 1928.)

China, mother of gardens. The Stratford Company, Boston, 1929. Plates.

Broad-leaved evergreens. (In Ladies' home journal, 1929, xlvi, 13.) Illustr.

Good shrubs for every garden. (In Ladies' home journal, 1929, xlvi, 203.) Illustr.

Shrubs to beautify the garden, spring, summer and autumn. (In Yearbook of the Garden Club federation of Massachusetts, 1929, i, 28–32.) Illustr.

Thomas Roland, 1863–1929. (In Yearbook of the Massachusetts horticultural society, 1930, p. 71.)

Aristocrats of the trees. The Stratford Company, Boston, 1930, Plates.

The island of Formosa and its flora. (In New flora and silva, 1930, ii, 92–103.)

Report on a journey around Gaspé Peninsula in search of the ragweed or hay fever plant. (Not yet published.)

The ragweed or hay fever plant. (Not yet published.)

A NEW ARUNDINARIA FROM CHINA

AIMÉE CAMUS

Arundinaria Fangiana, nov. subsp.

Culmi 0.30 m. alti, fistulosi, ramulis ad nodos fasciculatis. Folia chartacea, lanceolata, basi rotundata, in petiolum brevem attenuata, apice longe acuminata, 3–5 cm. longa, 0.4–0.7 cm. lata, glabra, margine scabra, nervis secundariis utrinque 3, venulis transversis conspicuis; vaginae elongatae, striatae, glabrae, superne truncatae, fimbriatae; ligulae truncatae. Panicula foliata, paucispiculata; pedicelli 1–1.7 cm. longi, glabri, tenues; spiculae 2–2.5 cm. longae, 6-florae, subglabra; glumae steriles contiguae, prima 0.5–2 mm. longa, ovata, acuminata; secunda 3–7 mm. longa, subulata, margine scabra; rachillae internodium 1 mm. longum, sericeum; gluma fertilis inferior ovato-lanceolata, apice cuspidata, 1.2–1.4 cm. longa, superne pilosula, 7-nervia nervis conspicuis, scabris. Palea 7–8 mm. longa, apice bicuspidata, subenervia, carinis ciliatis; rachillae internodia 4–6 mm. longa, sericea, superne dilatata; stamina 3; stylus longus; stigmata 2, elongata, plumosa. Caryopsis oblonga, superne attenuata, 6 mm. longa, sulcata, glabra.

SZECHUAN: Mt. Omei, alt. 3000–3300 m., *W. P. Fang*, no. 3002, August 15, 1920.

The leaves here described are those of flowering branches; those of sterile branches are probably much larger.

In the lower flower the fertile glume is 1.2–1.4 cm. long, in the second flower 0.8–1 cm.; the length decreases gradually toward the upper part of the spikelet.

In its general characters *A. Fangiana* approaches closely *A. racemosa* Munro to which, I believe, it should be attached as a subspecies. *Arundinaria racemosa* grows in the Northeast Himalayas, Nepal and Sikkim, at about the same altitude and differs from the Szechuan plant in the two glumes being very distant from each other and much smaller (2–3.5 cm. long), often less long cuspidate, in the internode of the rhachilla being much longer between the upper sterile glume and the first flower, often exceeding 2 mm., and finally in the often less long-cuspidate fertile glumes exceeding the palea not so much.

In *A. racemosa* the shape and size of the sterile glumes are very variable, but in all specimens which I have seen in the Paris Herbarium and in those of the Kew Herbarium the empty glumes are more distant and the upper glume is farther removed from the lower flower than in *A. Fangiana*. This character of the lengthening of the lower internodes of the rachilla seems constant.

I wish to thank Dr. Hill, Director of the Royal Botanic Gardens at Kew, for his kindness in having had compared the Chinese plant collected by Fang with the numerous specimens of *A. racemosa* in the Kew Herbarium.

Muséum d'histoire naturelle,
Paris.

CHROMOSOME STRUCTURE AND THE MECHANISM OF CROSSING OVER

Karl Sax

Plates 25 and 26

The correlation between the chromosome mechanism and the genetic behavior of hybrids is now so completely established that the chromosome theory of heredity is no longer questioned. There are, however, several important genetic facts which have no adequate cytological explanation. The cytological problems of greatest importance in connection with the chromosome theory of heredity are the maintenance of the linear order of the genes and the mechanism of crossing over.

The present study of meiotic chromosomes was undertaken primarily to determine the significance of spiral chromonemata. It was found that the coiling of the chromonemata is not a mechanism essential for the preservation of the linear order of the genes, as has been suggested by several investigators, but is due to a difference in the rate of contraction of the chromosome and the chromonema at certain stages of meiosis.

The organization of the chromatids in the chromosomes of *Secale* and *Lilium* was so different from that commonly found in Orthopteran chromosomes that a comparative study was made of the chromatids in certain plants and animals. The chromosome behavior is fundamentally the same in the plant and animal species, but in the plant chromosomes there is a much closer association of the paired chromatids, which at metaphase appear as a single coiled chromonema.

This work has lead to a cytological interpretation of crossing over which seems to be in accord with all genetic requirements.

MATERIALS AND METHODS

The figures on which the present study is based were from smear preparations of *Secale cereale* and *Lilium regale*. Pollen mother cells were smeared on a dry slide, fixed in Navaschin's solution, and stained with crystal violet iodine. Smears of the spermatocytes of the grasshopper, *Melanoplus femur rubrum*, were also studied.

In *Secale* it was difficult to get satisfactory figures of diplotene and early diakinesis stages. If the pollen mother cells were smeared thin enough for critical study, the cell walls were usually ruptured and the

chromatin was irregularly distributed among neighboring cells. Even in late diakinesis and metaphase the chromosomes may pass from one p. m. c. to another or be lost entirely, where the cells are subjected to too much pressure.

Throughout this paper the term chiasma will be used to mean the point where an exchange of partners occurs between the paired chromatids, and does not mean that a break has occurred as the original use of the term by Janssens would imply (Diagram 2).

Sister chromatids are those derived from a longitudinal splitting of one of the parental chromosomes. The association of homologous chromatids means that one chromatid from one parental chromosome is associated with a chromatid from the other homologous chromosome.

CHROMOSOME STRUCTURE IN SECALE

In the smear preparations it was not easy to get intact cells smeared sufficiently thin at the earlier stages of meiosis. The occasional critical figures obtained show that at pachytene there is an apparently split thread with pairs of chromomeres much like those pictured in *Lilium* by Belling (1928). Since the chromosomes appear to be double throughout most of their length at this stage, it is probable that they are longitudinally four-parted as Belling has described in *Lilium*.

At early diplotene the chromatids open out at various points forming the nodes and internodes so commonly seen in Orthopteran chromosomes. In *Secale* it was not possible to see the individual chromatids, but it is probable that the nodes and internodes represent exchange of partners among the chromatids. Possibly some of the apparent association between chromosomes may be due to twisting, but if so the twisting is slight as there is little evidence of it at later stages. There may be as many as four or five possible points of contact in a single chromosome at early diplotene as shown in figure 1.

The chromosomes shorten and thicken until at early diakinesis they appear as shown in figure 2, which represents three chromosomes from a single cell showing the typical structure at this stage. The loops have opened more fully and there are three or four points of contact which probably represent points where the chromatids exchange partners, although the relations of the chromatids at the chiasmas cannot be observed. There is no evidence of twisting of the chromosomes around each other in smear preparations, but in sectioned material such figures often show an apparent strepsinema condition. No internal structure of the chromosomes could be seen at this stage.

At late diakinesis the chromosomes have shortened and thickened further and the association between members of a bivalent is approximately the same as it is at metaphase. A typical chromosome at diakinesis is shown in figure 3. At this stage the chromosomes are usually attached only at the ends, although occasionally an additional median

attachment is evident. Occasionally there is an apparent separation of chromatids for a short distance at one end of the chromosome.

The seven haploid chromosomes of *Secale* vary somewhat in the location of spindle fiber attachment which results in various types of metaphase associations. The points of fiber attachment range from subterminal to median and are apparently constant for each chromosome. At early metaphase most, or often all, of the chromosomes are ring shaped, but at slightly later stages there may be as many as four pairs of chromosomes which are in contact at only one end. The seven pairs of chromosomes at metaphase are shown in figure 7, and are so arranged that the details of each one can be shown, which would not be possible if drawn in their natural positions. In all chromosomes there is a coiled chromonema, but no evidence of its dual nature except at the ends of certain chromosomes. Often one end appears to be in contact with no indication of a chiasma or exchange of partners among chromatids, while the other end shows the association between the homologous chromatids. In most cases where the spiral chromonemata could be followed, they appear to coil in opposite directions in the two homologues at metaphase, which means that when the homologues are side by side the coiling is in the same direction. Each homologue also has approximately the same number of coils. In some cases the chromonema seems to reverse its direction of coiling near one end.

The chromosome with the subterminal attachment is easiest to follow in respect to chromonema coiling. This chromosome at early metaphase is shown in figure 4. The coiling here is more uniform than is usual. At this stage the chromonema is finer and more coiled than at the later stages. In this figure, there are about six coils in each homologue. The points of attachment show no evidence of a previous chiasma or exchange of partners among chromatids.

More typical examples are shown in figures 5 and 6. In these chromosomes the coiling is not so uniform and apparent breaks occur in the chromonemata at about the points of the spindle fiber attachment.

In the early metaphase it is often difficult to differentiate the chromonema from the less chromatic portion of the chromosome. In these figures only the chromonemata are pictured, except in figure 16 where they are shown surrounded by the lighter staining constituent of the chromosomes. The less chromatic material extends to, but not beyond, the coiled chromonema which suggests that the coiled chromonema is limited by a definite sheath or pellicle. At the lower end of the chromosome represented in figure 6, the chromonema appears extended and free from any matrix as if the pellicle had broken at the end and released part of the coiled chromonema. Outside of the chromosome, whether it shows coiled chromonema or is homogeneous, there is a hyaline area which gives the impression that there is a limiting membrane at some distance from the chromatic material, but this appearance may be an optical illusion.

Only occasionally is there evidence of an unterminalized chiasma at metaphase. Figures 8 and 9 show exchanges of partners among the chromatids but there is no evidence that there is any fundamental difference between these chromosomes and those shown in figure 10, or in the last chromosome of figure 7. In figure 10 the exchange of partners simply forms a cross as the chromatids are pulled apart and there is no apparent crossing of chromatids.

At the later stages when some of the chromosomes are about to divide, the chromonemata become less coiled and appear more or less corrugated rather than spiral. In figures 10 and 12 the number of turns is reduced to two or three compared with five or six at the early stages. Meanwhile the length of the chromosomes is about the same, although the chromonemata appear to be somewhat thicker.

The separation of the chromatids in each chromonema appears to occur very rapidly and appears only after the chromonema is straightened out. The chromosome represented in figure 13 shows a separation of chromatids through about half the length of each homologue. Occasionally one homologue is split while the other is still slightly coiled and apparently undivided (Figure 14). The point of the spindle fiber attachment is especially clear in this figure. When the chromatids are entirely split in both homologues the chromosome appears much like those frequently found in most Orthoptera. A typical tetrad is shown in figure 15. The homologous chromatids are parallel and show no evidence of coiling at this stage.

When the chromosomes divide and pass to the poles, most of them are in the form of double V's held together only at the point of the spindle fiber attachment. These anaphase chromosomes seldom showed any internal structure in my preparations although occasionally some indication of a spiral chromonema could be observed (Figure 16). In this figure only one chromatid of each daughter chromosome is shown.

As the homologues reach the poles the split chromosomes elongate and the two members of each daughter chromosome separate widely except at the point of fiber attachment (Figure 17). When the nuclear wall is formed the chromosomes appear as long, more or less twisted, chromonemata held together by a still thinner constriction. The fiber constriction involves an appreciable portion of the two chromonemata. There is no true resting stage between the first and second meiotic division. Often the nuclei appear to contain an indefinite spireme stage, but it is always possible to identify some of the chromosomes and doubtless all of them retain their earlier association throughout this stage.

At the second division the chromosomes are shortened and the pairs of chromosomes lie parallel and more or less at right angles to the axis of the spindle fibers. No spiral chromonemata were observed during the second divisions, but it is quite possible that they exist. Although in the interphase the chromosomes are held together only at the point of spindle

fiber attachment, they show evidence of an attraction throughout their length at second metaphase and various degrees of association as the chromosomes are pulled apart (Figure 19). It is evident that at the second reduction division the chromosomes are not held together by the fiber attachment alone.

CHROMOSOME STRUCTURE IN LILIUM

The behavior of the chromosomes in the meiotic divisions of *Lilium* has been described by many investigators and only the more critical stages will be considered here.

As the four-parted chromosome reaches the diplotene stage and the chromatids open out, the chromonemata can be seen to be associated at a number of points. Most of these points probably represent points of exchange of partners among chromatids, although the individual chromatids could not be identified in my preparations at this stage (Figure 20). As the chromosomes shorten and are oriented on the first metaphase plate they show a reduction in the number of points of attachment. At this time there is an average of about two points of attachment for each chromosome. The orientation of the nodes and internodes is much like that found in the multiple ring chromosomes of certain Orthoptera. The looped internodes are usually more or less at right angles to each other. Such a chromosome with three nodes is shown in figure 21. The chromonemata are not clearly differentiated from the less chromatic substance in the chromosome at this stage, but do show evidence of a coiled structure. This coiled chromonema appears to be single at the earlier stages, but its double nature is indicated by the separation of the chromatids during the division of the chromosomes.

The chromosome represented by figure 22 has only two nodes and a comparatively long section of the chromonema between the fiber attachment end and the first node. If a chiasma has been partially terminalized prior to this stage, there should be some evidence of the dual nature of the chromonema at some point, which is not the case.

The nodes in *Lilium* are apparently points of exchange of partners among the four chromatids. The relation of the chromatids is shown in figure 23 where the chromatids are pulled out showing the chiasma. One of the paired chromosomes shows the separation of the chromatids. The other may be split, but in most cases the two daughter chromosomes lie in different planes more or less at right angles to each other so that the double nature of both chromosomes is not evident until the chromatids are widely separated.

The chromatids often vary in their rate of separation. One pair of chromatids may be completely pulled apart while the other is still coiled at the distal end (Figure 24). In these cases, one chromatid may be almost straight between the point of fiber attachment and the point where the chromatids are coiled together at their ends. The other

chromatids, which are separated at the distal ends and are not under tension, begin to form spirals or corrugations. This behavior is especially clear in figure 25, where two chromatids have separated and contracted into a more or less coiled structure while the other two chromatids are still associated and are relatively straight. Often all four chromatids are straightened out forming a distorted diamond-shaped tetrad. When the division is completed the chromatids of the daughter chromosomes contract and show more or less coiling as shown in figure 26. They are associated only at the point of spindle fiber attachment. Only chromosomes with a terminal fiber attachment are shown, although two of the twelve *Lilium* chromosomes have a sub-terminal attachment.

CHROMOSOME STRUCTURE IN MELANOPLUS

The spermatocyte chromosomes of *Melanoplus* are so similar to those described in other Orthoptera that a detailed description of them is unnecessary. The individual chromatids can be followed at all stages from diplotene to the end of the meiotic division. The chromatids are seldom so closely paired that they appear as a single chromonema. The chromatids shorten as the chromosome shortens between diplotene and metaphase so that during this period there is no coiling of the chromonema.

DISCUSSION

COILED CHROMONEMATA

The spiral structure of the chromonema was first described in 1880 by Baranetzky in *Tradescantia*. Since that time the spiral chromonemata of meiotic chromosomes have received little attention until recent years, although they were described in *Ascaris* and *Lilium* by Bonnevie (1908), and Vejdovsky (1912).

Coiled chromonemata in meiotic chromosomes have been described in *Tradescantia* by Sands (1923), Kaufmann (1926), Kuwada and Sugimoto (1926), Kuwada and Sakamura (1927), Sakamura (1927), and Clausen (1929). They have also been described in *Podophyllum* by Kaufmann (1926), in *Secale*, *Vicia*, *Fritillaria*, and *Lilium* by Sakamura (1927), in *Lathyrus* by Maeda (1928), in *Hosta* by Inariyana (1928), in *Lilium* by Belling (1928), in *Crepis* by Babcock and Clausen (1929), and in *Matthiola*, *Polemonium*, *Allium* and *Lathyrus* by Clausen (1929). The writer has also observed spiral chromonemata in *Pinus*, *Sambucus*, and *Triticum*.

According to Kuwada (1927), the coiled chromonemata in *Tradescantia* chromosomes at meiosis are double with the two chromatids so arranged that the two spirals can be easily separated without uncoiling. In most genera there is little evidence of the double nature of the chromonemata until late metaphase or early anaphase.

Spiral chromonemata have been described in a considerable number of representative genera and as the smear technique and proper differential staining comes into more general use, it is probable that most plant

genera will be found to have spiral chromonemata, at least in certain stages of meiosis. The fact that these structures are found in living cells and are so consistent in their form in a given genus, indicates that they are not artifacts produced by fixation. No doubt they are coagulated by fixation and may be greatly altered by certain reagents, but their definite organization and behavior must mean that the spiral chromonemata actually exist in the living chromosomes.

The behavior of the chromonemata, especially in *Lilium*, suggests that they possess the properties of a stiff elastic gel. When the coiled chromonema is stretched out at anaphase, it appears to contract and coil as soon as the tension is released when the chromatids finally separate (Figure 25). The contraction is not rapid since all stages of contraction can be observed in pollen mother cells from a single anther, but the behavior does suggest some elasticity of the chromonema.

In the earlier stages in both *Secale* and *Lilium*, the chromonemata lie in a matrix of lighter staining chromatic material, but when the chromatids are separated and elongated only the chromatids are differentiated from the cytoplasm. When the chromosomes shorten as they pass to the poles the less chromatic matrix is again visible (Figures 16 and 26). At a later stage when the daughter nuclei are organized, the *Secale* chromosomes again seem to consist of only the paired chromonemata (Figure 18). Bridges (Alexander 1928) suggests that the chromosome consists of a pellicle containing a chromonema of stiff gel coiled in a more fluid matrix. Such a chromosome sheath is described by Clausen (1929). A sheath, or limiting membrane, seems essential to account for the structures observed in the chromosomes.

THE SIGNIFICANCE OF SPIRAL CHROMONEMATA

According to Belling (1928), the chromonema of *Lilium* can contract to one-third of its original length before the chromomeres come in contact with each other. But the metaphase chromosome is only about one-tenth as long as the original chromonema at pachytene. Thus, in order to maintain the linear arrangement of the chromomeres a coiling or "zigzagging" is necessary at the later stages of contraction. The approximation of the chromomeres and the corrugation of the chromosomes are sufficient to account for all of the contraction observed according to Belling.

A similar explanation of chromosome coiling has been presented by Bridges (Alexander 1928) based on the description of chromosomes of *Ascaris* by Bonnevie (1908) and Vejdovsky (1912, 1926). Bridges assumes that the genes are in contact at all stages and that the gene string does not change its actual length by stretching or contraction except to a subordinate degree. The contraction of the chromosome would of course necessitate a coiling or looping of the chromonema which contains the gene string, if the linear arrangement of the genes is to be

maintained. Bridges accepts Kuwada's (1927) interpretation of the method of coiling. According to this interpretation the two chromatids of the chromonema coil in such a manner that for each turn of the spiral there is a twist of the two threads about each other in the reverse direction. Such a relation of the chromatids is essentially the same as a corrugation of two threads in only one plane. Such an arrangement of the chromatids permits free separation even though they may appear to be united in a single coil. This type of coiling would occur if the two chromatids are held fixed at the ends as the coiling occurs. Bridges assumes that coiling is caused by the contraction of the pellicle forcing the more or less elastic chromonema into a coil within the pellicle. The coiled condition is supposed to persist through metaphase and subsequent stages as pictured by Kuwada (1927) and Vejdovsky (1926).

In *Secale* there is evidence that coiling of the chromonema is caused by the contraction of the chromosome without any shortening of the chromonema. The chromosomes at metaphase are about one-third as long as they are at early diplotene while the chromonemata are about the same length at both stages (Compare Figures 1 and 4). At later stages, however, there is a shortening of the chromonemata while the chromosome length remains essentially unchanged. The spirals become fewer (Figures 12, 13, 14) and finally the chromatids appear as parallel rods (Figure 15). During the period from early metaphase to the stage where the chromosome shows its tetrad structure, the chromonema contract until they are about one-third as long as they were at early metaphase or early diplotene. Obviously, the coiling of the chromonemata is not a mechanism essential for the preservation of the linear arrangement of the genes.

In *Lilium*, the chromosomes at metaphase are about one-half as long as they are at diplotene. This shortening is associated with a coiling of the chromonemata which probably do not change their length to any great extent during this period. The length of the chromonemata at metaphase is about three times the length of the chromosomes which would mean that coiling begins when the chromonemata have decreased to about one-third of their original length, as Belling has found.

In *Lilium* the coiled chromonemata are found at all stages of the first meiotic division except for a short time when the chromatids are stretched out just before the final separation of the chromosomes. During metaphase the chromatids do contract somewhat but not more than one-half of their original length at diakinesis. When free from tension the chromatids are always coiled or corrugated at the first meiotic division.

The chromosomes of grasshoppers show approximately the same amount of contraction as found in *Secale* between diplotene and metaphase. There is, however, no coiling of the chromonema and the chromatids are easily identified as separate units through the various stages. At diakinesis and at metaphase of the meiotic divisions the chromatids

are so oriented in most cases that they are as free to separate as if they were parallel rods. In early prophase there is some evidence of a coiled structure but in the later stages the shortening of the chromosomes is accompanied by a corresponding shortening of the chromonemata.

A comparison of the behavior of the chromosomes in *Secale*, *Lilium* and Orthopteran species indicates that the coiling of the chromonema is due to the difference between the rate of contraction of the chromosome and the chromonema. In grasshoppers the chromonema shortens as the chromosome contracts; in *Secale* the chromosome shortens rapidly in the prophase while the chromonema is practically unchanged in length, but at metaphase the chromosome is unchanged while the chromonema shortens; and in *Lilium* the chromonema shortens somewhat, but is always longer than the chromosome except when it is stretched out at early anaphase. Possibly the rate of division has something to do with these differences. In the two species of plants the stages from diplotene to late diakinesis are not easily obtained but in grasshoppers these stages are the most common. A rapid contraction of the chromosome might prevent the corresponding change in the chromonema while a relatively slow change in chromosome length and organization would permit the chromonema to accommodate itself to this change.

If the spiral chromonema is the result of a contraction of the chromatids held in a relatively fixed position, then they would be free to separate while still coiled as Kuwada describes for *Tradescantia*. In *Secale*, however, the paired chromatids do not separate while coiled and in *Lilium* the paired chromatids separate only when pulled apart at time of division of homologous chromosomes. In *Lilium* the chromonema between the spindle fibre attachments and the first chiasma, is usually straightened out before any split appears. Occasionally the distal ends of the chromonema separate while still coiled, but in most cases the chromatids appear to be closely associated and pull apart only under considerable tension. However, the coiling must be primarily of the type described by Kuwada, which is essentially the same as a corrugation in one plane, or the chromatids would be so entangled that they could not be pulled apart at metaphase. It is probable, however, that some twisting of the chromatids occurs so that they are not easily separated while coiled.

CHROMATID ASSOCIATION

In both plants and animals the most critical studies indicate that the meiotic chromosomes consist of four chromatids at diplotene. In some animals the four chromatids can be followed through the prophase stages and "tetrads" are commonly observed at diakinesis and at metaphase. Even in the more complicated ring formations in the Orthoptera the four chromatids can be identified.

In most plants, however, the tetrad nature of the chromosome cannot be seen until late metaphase when the homologous chromosomes are

practically separated. The failure to recognize the tetrad structure of plant chromosomes until the late stages of the first meiotic division is evidently due to the close association and coiling of the paired chromatids.

According to Darlington (1929), homologous chromosomes at diakinesis and metaphase are held together only through the exchange of partners between pairs of chromatids. The chiasmas formed by exchange of chromatids evidently do hold the paired chromosomes together at the earlier stages, but at diakinesis and metaphase the homologous chromosomes are often associated where no chiasmas are present. In *Datura* there are no chiasmas at the late stages of the first meiotic division and the chromosomes are associated only at the ends (Belling 1927). In *Secale* many metaphase chromosomes are attached at one end with no apparent chiasma formation (Figures 4, 5 and 6). In many cases the chromosomes are in contact at their ends with no evidence of the existence of earlier chiasmas. Apparently the chromonemata can be attached at their ends without exchange of partners between pairs of chromatids. In *Lilium* the chromosomes at metaphase are apparently held together only by their chiasmas. The difficulty of separation of homologues seems to be dependent on the number of chiasmas present at metaphase. In *Secale* there is no evidence of unusual tension in the separation of homologues but in *Lilium* the paired chromosomes are pulled apart with some difficulty. Darlington finds that the short chromosomes with a single chiasma separate earlier than long chromosomes with several chiasmas.

Darlington's study of polyploid Tulips and Hyacinths does show that the degree of pairing of homologous chromosomes is dependent on the number of chiasmas formed at diplotene. Only two chromosomes can be associated at any one point at pachytene so that in triploids the homologous chromosomes always change partners. At diplotene only two chromatids are associated at any one point and the exchange of partners among chromatids forms the only connection between two or more homologous chromosomes. Darlington's explanation of the method of chromosome and chromatid association is of considerable value in interpreting the mechanism of crossing over and the chromosome behavior in polyploid species.

In triploids the bivalents are apparently separated with some difficulty at the first meiotic division while univalents appear to divide readily in most cases. Newton and Darlington (1929) suggest that the difference in the behavior of bivalents and univalents in triploids may be due to the differences in the constitution of the chromatids. In a bivalent the chromatids in each homologue may be from different parents, due to crossing over, while in a chromosome which has not been paired they are of the same origin. Occasionally a univalent appears to divide like a bivalent, but such a univalent may have been associated with the bivalents at an earlier stage so that it might consist of chromatids from different chromosomes.

According to Newton and Darlington (1929) the difficulty of separation of bivalent, and the ease of separation of univalent chromosomes must be due to a greater attraction between homologous chromatids than between sister chromatids. On purely *a priori* grounds there is no reason for supposing that such differences should exist. The fact that the chromatids are from different parents is no reason for supposing that they have a greater attraction for each other than chromatids from the same parent. In Orthopteran chromosomes, where the chromatids can be clearly observed, there is no indication that the association of sister chromatids is any different than the association of homologous chromatids. A stronger attraction between homologous chromatids than between sister chromatids would mean that only homologous chromatids would pair and as a result of such pairing no detectable crossing over could occur. Such an association is not in accord with genetic results in other genera.

The apparent difficulty of separation of bivalents compared with univalents is probably due to differences in the mechanical association of the chromatids. In *Lilium* the homologous chromonemata are coiled during metaphase and are connected by chiasmas. A single coiled chromonema would divide readily if the chromatids were associated according to Kuwada's interpretation, but the chromatids could not separate readily except in one plane. If these planes do not coincide in the bivalent then one pair of chromatids would separate only under considerable tension. There is evidence in *Lilium* that such differences between the two pairs of chromatids do exist (Figure 24). If there is any twisting of the homologues about each other, or if crossing over occurs, the difficulties in separation of coiled chromatids would be increased. In *Secale* the chromonemata are not coiled at the time of chromatid separation and the chiasmas are usually single and terminal. In these chromosomes there is no evidence that unusual tension is required to separate the chromosomes. The rare occurrence of univalents which behave like bivalents in the triploid Tulips and Hyacinths is probably due to some twisting of the chromatids about each other which would prevent easy separation.

PARASYNAPSIS AND TELOSYNAPSIS

In *Secale* and *Lilium* side by side pairing is essential to account for the relation of the homologues at diplotene and early diakinesis. The parasynaptic interpretation is the only one which is supported by cytological evidence in all genera which have been critically studied. The association of chromosomes in triploids described by Newton and Darlington (1929), and Belling's (1927) description of segmental interchange applied in more detail to the *Oenothera* problem of ring formation by Darlington (1929) has removed all remaining arguments for telosynapsis.

Recently telosynapsis has been described in *Secale* by Melburn (1929), but it is obvious from an examination of the figures presented that any conclusions drawn from such material are worthless.

PRE-REDUCTION OR POST-REDUCTION

The first meiotic division is generally considered to be the one at which the homologous chromosomes are usually separated (Wilson 1925, Robertson 1916), but there is good evidence that post-reduction also occurs (Wenrich 1916, Carothers 1926). When crossing over occurs there is little significance in these two terms because either meiotic division would be both reductional and equational for different segments of the same chromosome.

The invariable occurrence of pre-reduction must mean that sister chromatids are already bound together by the spindle fiber attachment at the leptotene or pachytene stage, or that the formation of nodes and internodes at diplotene is not a random process. The first suggestion is the more probable.

Where pre- and post-reduction occur in equal proportions in a particular chromosome (Wenrich, 1916) we must conclude that internode formation at diplotene depends on random association of chromatids and that the spindle fiber attachment does not unite associated chromatids until diplotene or later.

Invariable post-reduction will occur if homologous chromatids are bound together at the point of spindle fiber attachment at pachytene, or if internode formation is not a random process, but always occurs so that homologous chromatids are always associated at the point of fiber attachment. Post-reduction would also invariably occur if only homologous chromatids were paired, but in such a case crossing over could not be detected by genetic tests.

The fact that the chromosome segments are seldom, if ever, of the same genetic constitution at the point of the spindle fiber attachment in the "equational exceptions" described by Bridges and Anderson (1925) and by Redfield (1930) proves that in *Drosophila* the first meiotic division is invariably reductional. Both the cytological and the genetic evidence leads to the conclusion that regular post-reduction is exceptional.

THE MECHANISM OF CROSSING OVER

Janssens' earlier theory of crossing over has been discussed by Wilson and Morgan (1920) and his latest modification of the chiasmatype theory (Janssens 1924) has been considered in detail by McClung (1927). In his earlier discussion of crossing over Janssens assumed that the homologous chromosomes were twisted and broke at certain points of contact to reunite forming new associations which combined segments from each homologous chromosome. In his more recent paper he assumed that breaks might occur in the chromatids at any point where they were in contact. As the paired chromatids open out, the "chiasmas" represent points of segmental interchange between two homologous chromatids. Crossing over was described at various stages of meiosis including metaphase.

As Janssens' critics have pointed out, the chiasmatype theory of crossing over is not in accord with the cytological facts. The "chiasmas" are only optical phenomena and are formed by the alternate separation of different pairs of chromatids (Diagram 2). Since a detailed criticism of the chiasmatype theory of Janssens has already been presented by McClung it will be unnecessary to discuss it further at this time.

Belling (1929) has offered another explanation of crossing over, although it is presented only as a working hypothesis. He assumes that breaks occur in the chromatids at leptotene. When two breaks in different chromatids coincide at pachytene they may reunite to form a chiasma or point of segmental interchange between homologous chromatids. The chiasmas found at metaphase represent points at which crossing over occurs when the chromosomes divide.

As Newton and Darlington (1929) have pointed out Belling's theory of crossing over is based on the unproved assumption that the occurrence of one break will interfere with the occurrence of a second break in the adjacent sections of the chromatid. The theory can not be reconciled with the differences in chiasma formation in triploid and tetraploid Hyacinths (Darlington 1929). There is no explanation of the cause of numerous breaks in the chromatids, or if they do break, why they should reunite.

Morgan (1919) has suggested that the twisting of the chromosomes about each other in the early prophases might cause breaks in the chromatids so that sections of different chromatids would reunite. According to this theory crossing over is dependent on the twisting of chromonemata about each other at a number of points. This theory has little cytological support and does not meet all genetic requirements.

Several other theories have been presented to account for crossing over, but since they have such an inadequate cytological basis they need not be considered here.

In none of the theories presented is there an adequate explanation for the remarkable precision of crossing over so that duplication and deficiency of chromatid sections rarely occur. Nor is there any adequate reason why the chromatids should be recombined after they break.

No satisfactory interpretation of crossing over can be based entirely on the spermatocyte chromosomes of the Orthoptera, because in this group there is little cytological or genetic evidence that crossing over occurs in the males (McClung 1927, Nabours 1925). But if we assume, as seems probable, that chromosome behavior in plants and amimals is fundamentally the same, differing only in details, then our knowledge of Orthopteran chromosomes, combined with recent information concerning chromosome structure and behavior in plants, should serve as a basis for a logical interpretation of crossing over which is in accord with all genetic requirements.

The cytological interpretation of crossing over will be outlined, followed by the cytological evidence and a discussion of the genetic evidence.

THE CYTOLOGICAL INTERPRETATION OF CROSSING OVER

The homologous chromosomes become associated side by side at pachytene and are often more or less twisted about each other (Diagram 1). The chromonema of each chromosome is two-parted at leptotene although the sister chromatids may not be differentiated until pachytene or later. The pairs of chromatids may also be twisted about each other to some extent.

At diplotene the paired chromatids open out forming nodes and internodes. There is usually an alternate association of sister and homologous chromatids. The nodes represent points at which the chromatids change partners and are referred to as chiasmas. The maternal chromatids are pictured as black threads and the paternal chromatids as white threads (Diagram 2).

Between diplotene and metaphase the chromosomes contract about two-thirds of their length. In many species the paired chromatids do not contract during this period but form an apparently single spiral chromonema in each homologue. The relation of the chromatids during the earlier stages of chromosome contractions are shown in Diagram 3.

Due to the partial twisting of the chromosomes about each other at pachytene some of the internodes will be oriented so that two of the chromatids will come in contact where they cross each other at the chiasmas. Contact of chromatids at chiasmas will also occur due to the coiling of the chromonemata as shown in diagram 6. In this case the internodes open out at right angles to each other although only the sections of the chromonemata adjacent to the chiasma are represented. Beginning at the right end of this chromosome segment the coiling of both chromonemata is to the right, and at the chiasma the two crossed chromatids lie in one plane and are in contact with each other. Whether the chromatids come in contact due to twisting of the homologues or to coiling of the chromonemata, their subsequent behavior is the same. The paired chromatids on either side of the chiasma are closely associated and pairing of the chromatids, gene by gene, extends up to the point where the chromatids cross each other. The close association and coiling of the paired chromatids prevents any movement of the chiasmas and any strain imposed on the chiasma will cause the crossed chromatids to break at the point of contact. This strain on the chiasma could be induced by a further opening of the internodes, by unequal contraction of the two chromonemata, or by a slight amount of twisting of the chromonema as it coiled.

Breaks in the two chromatids occur at the same locus in most cases due to the close association of the paired chromatids. The free ends of the broken chromatids then pair, gene by gene, with the intact chromatids

until the broken segments of the different chromatids are brought in contact. In this way segments from different chromatids are combined.

Between early diplotene and metaphase the number of chiasmas is reduced, due to crossing over between different chromatids. In the chromosome represented by diagram 2, there are four chiasmas. Let us assume that crossing over occurs at chiasmas B and C. The relation of the chromatids at metaphase will then appear as shown in diagram 4. At this time, and probably at the earlier stages, the chromatids are so closely associated that they appear as a single coiled chromonema. In this diagram the association of maternal and paternal chromatids is indicated by cross lines.

The chiasmas which persist until metaphase are pulled apart as the chromosomes divide and at anaphase the four chromatids are completely separated except at the point of the spindle fiber attachment. The composition of the four chromatids resulting from this double crossover is shown in diagram 5. In the second division the chromatids, now the daughter chromosomes, are finally separated.

Crossing over between sister chromatids is not shown in the diagrams, but it could occur if there were preferential pairing between homologous chromatids, which is improbable. It could also occur if there were a twisting of the chromatids and pairing of homologous chromatids on either side of the twisted strands. Random association of chromatids, so that there is pairing between diagonal as well as adjacent chromatids, will result in crossing over between sister strands. With random associations of chromatids one-third of the crossovers should be between sister strands in diploids and one-fifth in triploids. Such a random association of chromatids is also improbable.

The present theory of crossing over is based on the fact that at diplotene there is an exchange of partners between paired chromatids at the chiasmas and that between diplotene and late diakinesis there is a reduction in the number of chiasmas. When extensive movement of the chiasmas is prevented by the close association or coiling of the paired chromatids, any reduction in the number of chiasmas must be due to breaks in the chromatids at the chiasmas so that segmental interchange occurs between two chromatids. This segmental interchange between two homologous chromatids is the cytological mechanism responsible for genetic crossing over.

THE CYTOLOGICAL EVIDENCE

The cytological evidence for this interpretation of crossing over is based on the work of McClung and his students with the Orthoptera, and on the recent work of Belling and Darlington, as well as the results of the present study of chromosome structure in *Secale* and *Lilium*.

In both plants and animals the homologous chromosomes pair side by side at the early prophase of the first meiotic division. The individual chromosomes may be longitudinally split before pairing as shown by

the work of Robertson (1916) and McClung (1928) and as indicated by the work on somatic chromosomes by Kaufmann (1926) and Sharp (1929). If the chromonema appears as a single thread at pachytene, which is often the case, the dual nature of the chromonema appears at later stages.

According to the cytological interpretation of crossing over two homologous chromatids must come in close contact with each other at chiasmas. This association of chromatids may be due to some twisting of the homologous chromatids about each other before or shortly after the diplotene stage, or to coiling of the chromonemata which would frequently cause the crossed chromatids to come in contact with each other at the chiasma. There is some evidence that a strepsinema stage occurs before or during early diplotene (Wenrich 1916, 1917, Robertson 1916, Janssens 1924). This twisting of the chromosomes occasionally persists to some extent to the later stages, but as a rule this torsion is undone as meiosis proceeds so that at metaphase the chromonemata on either side of a chiasma are in planes at right angles to each other. Strepsinema stages have also been described in many species of plants at both early and late prophase, but critical preparations show that twisting of synaptic chromosomes occurs only to a limited extent, if at all, at early and late diakinesis. Very little twisting of the chromosomes is necessary, however, to bring the crossed chromatids in contact at one or more chiasmas. Some such torsion seems necessary to produce apparently parallel chromosomes connected by a median chiasma as has been pictured at diakinesis in *Crepis* by Babcock and Clausen (1929).

There is no direct evidence that coiling of the chromonemata brings chromatids in contact at chiasmas, but there is adequate evidence that coiling of the chromonemata occurs in many plants and some animals. By means of wire models it can be demonstrated that such coiling will often bring the crossed chromatids into close contact at the chiasmas (Diagram 6).

In the Orthopteran chromosomes the associated chromatids change partners so that at diplotene different chromatids are paired in alternate internodes. The relation of the chromatids at diplotene is not so clear in plant chromosomes, but there is some evidence that the nodes are really chiasmas at this stage, and at metaphase when the chromosomes are pulled apart the chiasmas are frequently observed. It seems very probable that the relation of the chromatids at diplotene is the same in most plant and animal species.

There is no coiling of the chromonemata in the Orthopteran chromosomes at diplotene or later stages and the chromatids appear to be free to divide in a single plane. As the chromosome contracts and the diplotene loops open out, the chiasmas are free to move along the chromosome and are easily terminalized. In these chromosomes there is little chance for crossing over to occur.

In many plants and apparently in some animals the chromatids are closely associated and are coiled. In such chromosomes there can be no extensive movement or terminalization of the chiasmas before late metaphase. But there is a reduction of the number of chiasmas between diplotene and metaphase. In *Lilium* the total number of nodes or chiasmas is reduced from about thirty-nine at diplotene to about twenty-three at late diakinesis and metaphase (Belling 1928). A similar reduction of the number of chiasmas is also shown in *Tulipa* by Newton (1927). In *Secale* the average number of chiasmas in typical chromosomes is reduced from about four at diplotene to one or two at metaphase. The subterminal chiasmas in *Secale* are often terminalized but the median ones must break at the point of intersection of the crossed chromatids. If terminalization had occurred the dual nature of the chromonemata should be evident in the median sections of the chromosomes as it is occasionally at the ends.

The reduction in the number of chiasmas in these species must mean that in most cases the chiasmas which disappear between diplotene and diakinesis are due to breaks in the crossed chromatids. According to Belling (1928) "the nodes which disappear between diplophase and late diakinesis do not seem to be all or mainly twists. Nor do these vanishing nodes seem to be chiasmas which open out; for if so, this process should have been visible as it is at early anaphase." As has been shown in the diagrams such breaks would result in crossing over between two chromatids.

In some chromosomes as many as three or four crossovers are possible, although it is improbable that so many chiasmas would break at one division of a single chromosome. The average number of crossovers per chromosome appears to be about two in *Secale* and somewhat more than one in *Lilium* and *Tulipa*. Some of these crossovers may be between sister chromatids and could not be detected by genetic tests.

The cytological evidence for crossing over is not complete in all details and the actual breaks in the chromatids at chiasmas have not yet been observed. It seems very probable, however, that crossing over between homologous chromatids is associated with the reduction in the number of chiasmas between diplotene and diakinesis as Darlington (1929) has suggested.

THE GENETIC EVIDENCE

The genetic evidence for crossing over, especially in *Drosophila*, is now so complete that any theory regarding the mechanism involved can be thoroughly tested. The cytological interpretation presented in the preceding section seems to be in accord with the genetic results.

Time of Crossing Over

According to the genetic evidence crossing over must occur shortly after the pairing of homologous chromosomes. The cytological evidence

presented in the preceding section indicates that it occurs between diplotene and diakinesis. The effect of temperature on crossing over would seem to show that the segmental interchange between chromatids occurs at an early prophase stage (Plough, 1917). The potential amount of crossing over is determined to some extent by the number of chiasmas formed at early diplotene so that any treatment which would affect chiasma formation at this time might be correlated with the amount of crossing over, even though the actual breaks at the chiasmas do not occur until late diplotene or early diakinesis.

Crossing over occurs at the four-strand stage as was shown by Bridges (1916). Several cases of equational non-disjunction were found where one of the X chromosomes was a crossover and the other was not. Later this interpretation was more fully confirmed by an analysis of equational exceptions obtained from triploid females of *Drosophila* (Bridges and Anderson 1925). These results clearly indicate that crossing over occurs when the chromosomes are split into two strands or chromatids. This work also proves that crossing over occurs only between two chromatids at any one point. The present cytological interpretation is in accord with these genetic results, but the previous theories are not.

Gene Duplication and Deficiency

Crossover levels between the two chromatids seem to be remarkably uniform, but Sturtevant (1925) has found a case of unequal crossing over at the bar locus of the X chromosome in *Drosophila*. If the paired chromatids are not closely associated on either side of a chiasma it is possible for the crossed chromatids to come in contact so that a break will result in unequal crossing over. Such a relation of the chromatids and the results of unequal crossing over are shown in diagrams 7 and 8.

Sturtevant found that the order of the different genes was unchanged in duplicated and deficient sections of the chromosomes but the order of the two alellomorphs, bar and infrabar, may be BB′ or B′B. The order of alellomorphic genes will depend on the point at which unequal crossing over occurs.

Sturtevant's data indicate that the length of the chromosome is increased by duplication because the percentage of crossovers between forked and fused in normal bar stock is 2.5, but when the bar locus is double in each chromosome the percentage of crossing over between forked and fused is increased to 3.5. Apparently the unequal crossing over in this case involves an average length of one genetic unit.

Subsequent pairing between duplicated and deficient chromosomes will involve difficulties in the pairing of similar genes, although the elasticity of the chromonemata might permit pairing of similar genes in cases where only a very short section is involved.

The most remarkable fact concerning crossing over is the accuracy of chromatid exchange at the same level. The unequal crossing over at

the bar locus described by Sturtevant is exceptional, and is the only case recorded. Equal crossing over would be expected to occur if the associated chromatids are paired, gene by gene, up to the point of crossing of chromatids. This close association of the paired chromatids on either side of the chiasma would result in very short sections of the chromatids where crossing over is free to occur. In fact the pairing of similar genes in the associated chromatids would be expected to bring the point of crossing over to a region between the same two consecutive genes in each of the two chromatids involved in crossing over. The fact that the chromatid can contract about two-thirds of its length between diplotene and late metaphase suggests that at the time of crossing over, the gene elements may be separated by genetically inactive segments of the gene string.

Crossing over between Sister Chromatids

Crossing over between sister chromatids can only be detected by genetic tests in case of unequal crossing over, or perhaps by comparing the amount of crossing over in diploids and in triploids. Sturtevant (1928) has found no case of unequal crossing over at the bar locus of the X chromosome which is not accompanied by crossing over between forked and fused, so he concludes that in this region of the X chromosomes crossing over between sister chromatids does not occur. If pairing occurs between chromatids at random at the prophase of the meiotic division, then one-third of the crossovers in diploids and one-fifth of the crossovers in triploids will be between sister chromatids. A comparison of crossing over frequency in diploids and triploids should show whether or not crossovers occur between sister strands, but as Anderson and Bridges (1925) and Redfield (1930) have found, the differences between diploids and triploids show so much variation in different regions of the chromosome that any differential effect on crossing over, which might be caused by crossing over between sister chromatids, is completely masked.

There is no genetic evidence that crossing over occurs between sister chromatids, and the cytological evidence indicates that such crossing over must be exceptional. Crossing over between sister chromatids posits preferential pairing of homologous chromatids which is unlikely, and if such pairing is exclusive no genetic crossovers would occur. An occasional crossover between sister chromatids might be expected, due to the association of different homologous chromatids in two successive internodes, but such crossovers must be considered exceptional.

Interference

The phenomenon of interference was first observed by Sturtevant in 1913 and since that time it has been extensively studied by a number of investigators (Morgan, Bridges, and Sturtevant, 1925). In *Drosophila* chromosomes there is a modal interval between crossovers so that a break in one region interferes with a second break. Zero coincidence is found

for a certain distance, followed by an increase and then a second decrease, due to a second point of crossing over. The amount of coincidence is different for the three long chromosomes and varies in different sections of the same chromosome. The relation of the chiasmas and internodes seems to provide an adequate cytological explanation of interference. The genetic evidence indicates that the distance between crossovers is variable and Bellings (1928) description of *Lilium* chromosomes shows that the internode length is variable. The high coincidence in the middle of the third chromosome of *Drosophila* indicates that breaks in chiasmas are more likely to occur in two consecutive chiasmas where the internode length is comparatively long.

Variations in Crossing over

The amount of crossing over varies in different chromosomes and in different sections of the same chromosome (Morgan, Bridges, and Sturtevant, 1925). Crossing over would be expected to be a variable process if chiasmas are formed more or less at random and break only as the result of accidental twisting, unequal chromonema contraction, or other irregularities. Both the genetic and the cytological evidence is in accord with Morgan's (1925) conclusion that crossing over is an accidental by-product of the reduction division.

In *Drosophila* crossing over does not occur in the male and may be partially or completely inhibited in the female. There are several possible explanations to account for the lack of crossing over in the male. If only sister chromatids are associated at diplotene, there would be no chiasma formation and no opportunity for crossing over to occur. But due to absence of chiasma formation the association of homologues would be loose and considerable irregularity would be expected in the first meiotic division. There is adequate genetic and cytological evidence that such irregularity does not occur. Random pairing between only homologous chromatids would also prevent any detectable crossing over, but there is no reason to suppose that such pairing occurs, or if it occurs, why it should not occur in the female as well as the male. The only alternative seems to be that the association of the chromatids in the male is the same as in the female, but that in the male the chromatids can adjust themselves to changes in the chromosome during meiosis without breaking at the chiasmas as appears to be the case in the Orthoptera[1].

The Y chromosome of *Drosophila* is a special case because it shows no crossing over with the X even when it is present in the female (Bridges 1916). In secondary non-disjunction of an XXY female Bridges finds that pairing between XX occurs about four times as often as between XY. This difference in pairing of the X and Y chromosomes indicates that there is less attraction between the X and Y than between the X chromo-

[1]Huettner's description of the spermatocyte chromosomes of *Drosophila* which appears in a recent issue of the Zeit. f. Zellforschung indicates that there is a loose association of homologous chromosomes, but that a few chiasmas are formed and the first meiotic division is regular.

somes. Such a difference may be due to the absence of genetic factors, or it would occur if chromatid pairing in the Y is always between the sister chromatids. If only sister chromatids pair the X and Y could be associated only at the ends, which would result in loose pairing of the X and Y in normal males so that these chromosomes should divide before the division of the autosomes or tend to lag behind as univalents. Metz (1926) has found in several species of *Drosophila* that there is a loose association of the X and Y chromosomes at meiosis. According to Huettner (1930) the X and Y lag behind in the first spermatocyte division of *Drosophila melanogaster*, although apparently not as univalents.

Where crossing over is suppressed in all chromosomes of the female (Gowen and Gowen 1922), it is possible that pairing occurs only between sister chromatids. As has previously been pointed out, such pairing would result in a loose association of homologous chromosomes with the frequent occurrence of univalents at the first meiotic division and considerable irregularity in chromosome distribution. Gowen (1928) does find a relatively high proportion of chromosome duplication in the progeny of non-crossover flies.

This interpretation of the cause of no crossing over is supported by the work of Beadle (1930). He found that a single recessive factor caused asynapsis, or lack of chromosome pairing at meiosis, in *Zea*. The pollen of such plants is sterile, but some of the ovules are functional. When these asynaptic plants are pollinated with normal pollen about half of the progeny were triploids. Asynapsis leads to triploid production in *Zea* and is probably the cause of triploid flies in Gowen's non-crossover stock.

Asynapsis would occur if there is a differential rate of development between chromosome pairing and chromatid organization. If at leptotene the sister chromatids have already reached a stage of separation and development commonly found at diplotene then there can be no chiasma formation at later stages because the sister chromatids are already organized in pairs. The pairing between homologous chromosomes would be very loose, if it occurred at all. As a result no crossovers would occur, univalents would usually be found at diakinesis and metaphase, and irregular distribution of univalents would produce gametes with the haploid, intermediate, and diploid chromosome numbers. Asynaptic females crossed with normal males would produce aneuploid and triploid progeny. Apparently the pairing of sister chromatids in non-crossover stocks of *Drosophila* is not exclusive because rare crossovers are obtained (Gowen, 1929). In Beadle's asynaptic strain of *Zea* a few bivalents are often found.

A considerable number of crossover modifiers have been found in *Drosophila* which decrease or eliminate crossing over in certain chromosome segments (Morgan, Bridges, and Sturtevant, 1925). These variations in crossing over may also be due to preferential pairing of sister chroma-

tids in these regions. If preferential pairing of sister chromatids occurs over a considerable portion of the chromosome there should be a loose association of the homologues, and crossing over should be reduced or eliminated from a relatively long section of the chromosome. Bridges' (1916) work on high non-disjunction stocks of *Drosophila* seems to be of value in solving this problem. According to Bridges a high percentage of non-disjunction exceptions from XXY females means that the percentage of XY pairing is increased while pairing between XX is decreased. This change in the relations of the X and Y chromosomes would be expected if a genetic factor caused preferential pairing of sister chromatids for a considerable length of the X chromosome. The association between X chromosomes would be decreased because few chiasmas would be formed. The loose association between the two X chromosomes would result in an increase of XY pairing, which normally is very low. But such an association of sister chromatids would also decrease the amount of crossovers between the X chromosomes which do pair. It is perhaps significant that Bridges found crossover reducers in high non-disjunction stocks which decreased the amount of crossing over in the X chromosomes (Morgan, Sturtevant, and Bridges, 1925).

Crossing over would also be eliminated in chromosome segments if a chromosome with an inverted segment paired with a normal chromosome as Sturtevant (1926) has found. The cytological explanation is obvious.

Crossing over in Triploids

If the present cytological interpretation of crossing over is correct it must also be in accord with the crossover relations found in triploids. In triploid females of Drosophila crossing over has been found to occur between all three of the X chromosomes (Bridges and Anderson 1925) and between the three third chromosomes (Redfield 1930). In both cases two types of double crossovers were found; recurrent crossovers where the second crossover involves the same two chromosomes as the first, and a progressive type in which the second crossover takes place between different chromosomes from the first. These two types of crossovers occur with equal frequency. Appropriate genetic tests have permitted an analysis of the two chromosomes which pass to the same egg cell.

The behavior of the chromosomes in triploid Hyacinths described by Darlington (1929) seems to offer an explanation of triploid crossing over. When three homologous chromosomes pair at pachytene only two of them are associated at any one point so that an alternation of partners occurs. The association of three such homologous chromosomes at pachytene is represented by diagram 9. At diplotene chiasmas are formed between any two of the three chromosomes as shown in diagram 10. At the first reduction division two of the three chromosomes pass to one pole. The equational division separates paired chromatids.

In the hypothetical trivalent, shown in diagram 10, let us assume that crossovers occur at chiasmas 1, 3, and 5. The spindle fiber attachment is at the left end. We will assume that chromosomes A and B pass to the same pole at the first meiotic division. The chromatid constitution for the different segments of these two chromosomes will be $\frac{\text{AAAA}}{\text{ABBB}}$ and $\frac{\text{BAAC}}{\text{BBCA}}$. The second reduction division will then separate paired chromatids so that the two chromatids received by the egg cell will be $\frac{\text{AAAA}}{\text{BAAC}}$, or $\frac{\text{AAAA}}{\text{BBCA}}$ or $\frac{\text{ABBB}}{\text{BAAC}}$ or $\frac{\text{ABBB}}{\text{BBCA}}$. Three of these associations of chromatids would result in "equational exceptions" since for part of their length the two chromatids are alike. Crossing over between three chromosomes may be progressive or recurrent. In the above case only progressive crossovers occur, but if chromosome C paired with A instead of B, which would be equally probable, then recurrent crossovers would be obtained. With random association of the three homologous chromosomes, recurrent and progressive crossovers should occur in equal numbers.

In both the X and the third chromosome of *Drosophila*, regions in which the genes are closely spaced on the diploid map are lengthened on the triploid map, and regions in which the genes are far apart in the diploid are shortened in the triploid. The work of Muller and Painter (1929) and of Dobzhansky (1930) seems to throw some light on the possible cause of these differences in crossing over. These investigators found, that in the third chromosome the regions where the genes are closely spaced on the genetical map are far apart on the cytological map and *vice versa*. Such a relationship suggests that in regions where the genes are closely spaced on the genetical map, the average internode length between chiasmas is relatively long. The occurrence of long internodes would indicate that there is preferential pairing of chromatids in such regions. Such preferential pairing is probably caused by the physical relations of the chromosomes at the time of pairing rather than any preferential attraction between different chromatids.

When three chromosomes pair there may be preferential pairing of two chromosomes in the region where long internodes occur in diploids or the chromosomes may change partners in this region. In either case the number of chiasmas will be increased in this region in the triploid. In the trivalent shown in diagram 10, let us assume that in the diploid the internode length frequently extends from chiasma 1 to chiasma 4. In the triploid two additional chiasmas are formed in this region. Thus crossing over in triploids would be increased in regions where genes are closely spaced in the diploid.

In regions where the internode lengths are short in the diploid the intercalation of the third chromosome between two chiasmas would not

be expected to occur, so that for regions where the genes are widely spaced on the diploid map crossing over in the triploid would be reduced one-third.

SUMMARY

In *Secale cereale* each of the homologous chromosomes at metaphase of the first meiotic division contains a single coiled chromonema. The direction of coiling of the chromonema, in respect to the point of spindle fiber attachment, seems to be the same for any two homologous chromosomes.

During metaphase the chromonemata contract and become uncoiled. The chromonemata do not divide into separate chromatids until the chromonemata are uncoiled, although doubtless the two chromatids retain their identity from early prophase.

Between diplotene and metaphase the chromosomes shorten about one-third, but the chromonemata retain their original length by coiling. During metaphase the length of the chromonema is reduced about one-third while the length of the chromosome remains essentially the same.

In *Lilium regale* coiled chromonemata are also found at metaphase. The first meiotic division begins while the chromonemata are coiled. As the chromosomes are pulled apart the spindle fiber ends of the chromonemata are straightened out. The chromosomes are apparently separated with difficulty. When the division is nearly completed the chromonemata are pulled out into more or less straight rods. At this time the two chromatids of each chromonema can be identified. When the division is complete the chromatids contract and become more or less coiled. At early telophase each daughter chromosome appears as two coiled chromatids held together only at the point of the spindle fiber attachment. During metaphase and anaphase there is some shortening of the chromonemata but it is always longer than the chromosome when free from tension.

The coiling of the chromonemata, in *Secale* at least, is not a mechanism essential for the preservation of the linear order of the genes.

A comparison of *Secale* and Orthopteran chromosomes indicates that coiling of the chromonema is due to a differential rate of contraction between the chromosome and the chromonema.

The relations of the chromatids during the meiotic divisions are fundamentally the same in both plant and animal chromosomes. The nodes, or chiasmas, represent points where the chromatids exchange partners.

In plants the individual chromatids are closely associated in an apparently single chromonema and the tetrad nature of the bivalent chromosome is not clearly evident until late metaphase or anaphase.

Between early diplotene and late diakinesis the number of chiasmas is reduced, due primarily to breaks in the chiasmas. Such breaks would result in crossing over between the two chromatids involved.

A cytological interpretation of crossing over has been presented, based on the reduction in numbers of chiasmas between diplotene and late

diakinesis. This interpretation of crossing over seems to be in accord with all of the genetic requirements.

The genetic phenomena of interference, gene duplication and deficiency, variations in crossing over, and crossing over in triploids, have been discussed in their relation to the cytological mechanism of crossing over.

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LITERATURE CITED

Alexander, J. (1928). Colloid Chemistry. Vol. ii. p. 1029. The Chemical Catalogue Co. New York.

Belling, J. (1927). The attachments of chromosomes at the reduction division in flowering plants. (Journ. Gen. **18**: 177–205.)

Belling, J. (1928). The ultimate chromomeres of *Lilium* and *Aloe* with regard to the number of genes. (Univ. Calif. Pub. Bot. **14**: 307–318.)

Belling, J. (1928). Contraction of chromosomes during maturation divisions in *Lilium* and other plants. (Univ. Calif. Pub. Bot. **14**: 335–343.)

Belling, J. (1928). A working hypothesis for segmental interchange between homologous chromosomes in flowering plants. (Univ. Calif. Pub. Bot. **14**: 283–291.)

Belling, J. (1928). Nodes and chiasmas in the bivalents of *Lilium* with regard to segmental interchange. (Biol. Bull. **54**: 465–470.)

Babcock, E. B. and Clausen, J. (1929). Meiosis in two species and three hybrids of *Crepis* and its bearing on taxonomic relationship. (Univ. Calif. Pub. Agr. Sci. **2**: 401–432.)

Baranetzky, J. (1880). Die Kerntheilung in der Pollenmutterzellen einiger *Tradescantien*. (Bot. Zeit. **38**: 241–247, 265–274, 281–295.)

Beadle, G. W. (1930). Genetical and cytological studies of Mendelian asynapsis in *Zea mays*. (Cornell Univ. Mem. **129**: 3–23.)

Bonnevie, K. (1908). Chromosomenstudien, 1. Chromosomen von *Ascaris*, *Allium* und *Amphiuma*. (Arch. Zellforsch. **2**: 201–278.)

Bridges, C. B. (1916). Non-disjunction as proof of the chromosome theory of heredity. (Genetics, **1**: 1–52, 107–163.)

Bridges, C. B. and Anderson, E. G. (1925). Crossing over in the X chromosomes of triploid females of *Drosophila melanogaster*. (Genetics **10**: 418–441.)

Carothers, E. E. (1926). The maturation divisions in relation to the segregation of homologous chromosomes. (Quart. Rev. Biol. **1**: 419–435.)

Clausen, J. (1929). Exchange between chromatids of homologous chromosomes. (Reviewed in Res. Genetica **4**: 252.)

Darlington, C. D. (1929). Meiosis in polyploids. II Aneuploid Hyacinths. Journ. Gen. **21**: 17–56.)

Darlingtion, C. D. (1929). Ring formation in *Oenothera* and other genera. (Journ. Gen. **20**: 345–363.)

Darlington, C. B. (1929). Chromosome behavior and structural hybridity in Tradescantiae. (Journ. Gen. **21**: 207–286.)

Dobzhansky, T. (1930). Translocations involving the third and the fourth chromosomes of *Drosophila melanogaster*. (Genetics, **15**: 347–399.)

Gowen, J. W. (1919). A biometrical study of crossing over. (Genetics, **4**: 205–250.)

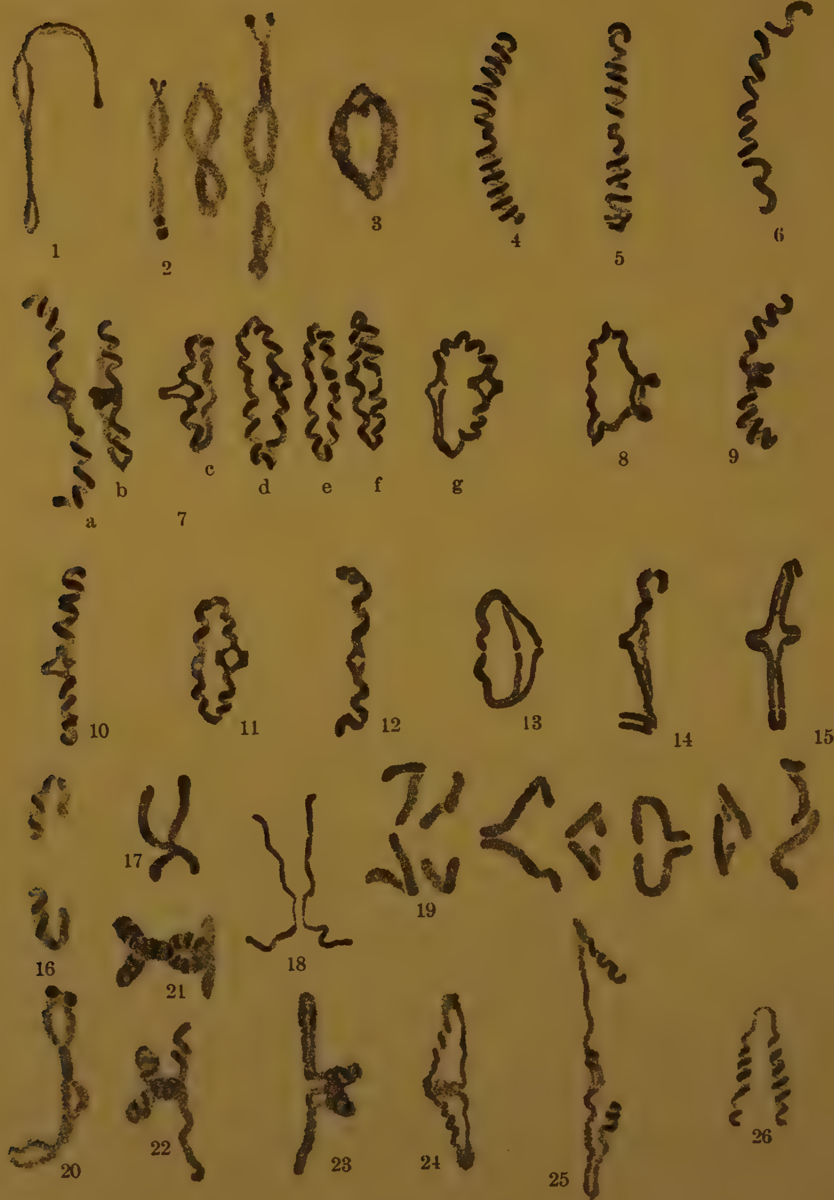
Gowen, M. S. and Gowen, J. W. (1922). Complete linkage in *Drosophila melanogaster*. (Amer. Nat. **56**: 286–288.)

Gowen, J. W. (1928). Mutation, chromosome non-disjunction and the gene. (Science, N. S. **68**: 211–212.)

Gowen, J. W. (1929). The cell division at which crossing over takes place. (Proc. Nat. Acad. Sci. Wash. **15**: 266–268.)

Huettner, A. F. (1930). Recent criticisms concerning meiosis in *Drosophila melanogaster*. (Science, **71**: 241–243.)

INARIYAMA, S. (1928). On the spiral structure of chromosomes in *Hosta Sieboldiana* Engl. (Bot. Mag. Tokyo, **42**: 486–489.)
JANSSENS, F. A. (1924). La chiasmatypie dans les insects. (La Cellule, **34**: 135–360.)
KAUFMANN, B. P. (1926). Chromosome structure and its relation to the chromosome cycle. 1. Somatic mitoses in *Tradescantia pilosa*. (Amer. Journ. Bot. **13**: 59–80.)
KAUFMANN, B. P. (1926). Chromosome structure in its relation to the chromosome cycle. II. *Podophyllum peltatum*. (Amer. Journ. Bot. **13**: 355–63.)
KUWADA, Y. AND SUGIMOTO, T. (1926). On the structure of the chromosomes in *Tradescantia virginica*. (Bot. Mag. Tokyo, **40**: 19–20.)
KUWADA, Y. AND SAKAMURA, T. (1927). A contribution to the colloid chemical and morphological study of chromosomes. (Protoplasma **1**: 239–254.)
KUWADA, Y. (1927). On the spiral structure of chromosomes. (Bot. Mag. Tokyo, **41**: 100–109.)
MAEDA, T. (1928). The spiral structure of chromosomes in the Sweetpea (*Lathyrus odoratus*, L.). (Bot. Mag. Tokyo, **42**: 191–195.)
McCLUNG, C. E. (1927). The chiasmatype theory of Janssens. (Quart. Rev. Biol. **2**: 344–366.)
McCLUNG, C. E. (1928). Differential chromosomes of *Mecostethus gracilis*. (Zeit. Zell. v. m. Anat. **7**: 756–778.)
MELBURN, M. C. (1929). Heterotypic prophases in the absence of chromosome pairing. (Nat. Res. Council Canada **1**: 512–527.)
METZ, C. W., (1926). Observations on spermatogenesis in *Drosophila*. (Zeit. f. Zell. u. Mik. Anat. **4**: 1–28.)
MORGAN, T. H. (1919). The physical basis of heredity. 305 pp. I. B. Lippincott Co., Philadelphia.
MORGAN, T. H., BRIDGES, C. B. AND STURTEVANT, A. H. (1925). The genetics of *Drosophila*. (Biblio. Gen. **2**: 1–262.)
MORGAN, T. H. (1925). The bearing of genetics on cytological evidence for crossing over. (La Cellule, **36**: 113–123.)
MULLER, H. J. AND PAINTER, T. S. (1929). The cytological expression of changes in gene alignment produced by X-rays in *Drosophila*. (Amer. Nat. **63**: 193–200.)
NABOURS, R. K. (1925). Studies of inheritance and evolution in Orthoptera. V. The grouse Locust, *Apotettix Eurycephalus* Hancock. (Kan. Agr. Exp. Sta. Tech. Bull. **17**: 3–231.)
NEWTON, W. C. F. (1927). Chromosome studies in *Tulipa* and some related genera. (Journ. Linn. Soc. **47**: 339–354.)
NEWTON, W. C. F. AND DARLINGTON, C. D. (1929). Meiosis in polyploids. (Journ. Gen. **21**: 1–55.)
REDFIELD, HELEN, (1930). Crossing over in the third chromosome of triploids of *Drosophila melanogaster*. (Genetics, **15**: 205–252.)
ROBERTSON, W. R. B. (1916). Chromosome studies. 1. (Jour. Morph. **27**: 179–332.)
PLOUGH, H. H. (1917). The effect of temperature on crossing over in *Drosophila*. (Jour. Exp. Zool. **24**: 147–209.)
SAKAMURA, T. (1927). Fixierung von Chromosomen mit siedenden Wasser. (Bot. Mag. Tokyo, **41**: 59–64.)
SAKAMURA, T. (1927). Chromosomenforschung an frischen material. (Protoplasma **1**: 537–565.)
SANDS, H. (1923). The structure of the chromosomes in *Tradescantia virginica* L. (Amer. Journ. Bot. 10: 343–360.)
SHARP, L. W. (1929). Structure of large somatic chromosomes. (Bot. Gaz. **88**: 349–382.)
STURTEVANT, A. H. (1925). The effects of unequal crossing over at the bar locus in *Drosophila*. (Genetics, **10**: 117–147.)
STURTEVANT, A. H. (1926). A cross-over reducer in *Drosophila melanogaster* due to inversion of a section of the third chromosome. (Biol. Zbl. **46**: 697–702.)
STURTEVANT, A. H. (1928). A further study of the so-called mutation at the bar locus of *Drosophila*. (Genetics, **13**: 401–409.)



Chromosome structure

Vedjovsky, F. (1912). Zum Problem der Vererbungsträger. (Böhm. Ges. Wiss. Prag, p. 1–184.)
Vejdovsky, F. (1926). Structure and development of the "Living Matter." p. 360. Royal Bohemian Soc. Sci. Prague.
Wenrich, D. H. (1916). The spermatogenesis of *Phrynotettix magnus* with special reference to synapsis and the individuality of chromosomes. (Bull. Mus. Comp. Zool. **60**: 57–133.)
Wenrich, D. H. (1917). Synapsis and chromosome organization in *Chorthippus* (*Stenobthrus*) *curtipennis* and *Trimerotropis suffusa* (Orthoptera). (Jour. Morph. **29**: 471–516.)
Wilson, E. B. and Morgan, T. H. (1920). Chiasmatype and crossing over. (Amer. Nat. **54**: 193–219.)
Wilson, E. B. (1925). The cell in development and heredity, p. 1232. The Mac Millan Co., New York.

DESCRIPTION OF PLATE 25

All figures were drawn from smear preparations of pollen mother cells. Figures 1 to 19 inclusive are magnified 2700 times; figures 20 to 26 inclusive are magnified 1600 times.

Secale cereale

Fig. 1. A typical chromosome at diplotene showing nodes and internodes.
Fig. 2. Three chromosomes at early diakinesis showing the number and distribution of nodes and internodes.
Fig. 3. A typical association of homologues at late diakinesis.
Figs. 4–6, Metaphase chromosome with coiled chromonemata.
Fig. 7. All seven chromosomes at metaphase showing the different types of chromosome pairing.
Fig. 8. A vertical ring chromosome with a chiasma at one end.
Figs. 9–12. Chromosomes at late metaphase showing less coiling of the chromonemata and the dual nature of the chromonemata.
Fig. 13–15. Chromosomes at late metaphase showing the straightening of the chromonemata and the separation of the chromatids.
Fig. 16. Two chromatids at late anaphase.
Fig. 17. A daughter chromosome at telophase.
Fig. 18. A chromosome at interphase. The two chromatids are held together only by the spindle fiber attachment.
Fig. 19. The seven chromosomes at the second meiotic division.

Lilium regale

Fig. 20. A chromosome with nodes and internodes at diplotene.
Figs. 20–22. Metaphase chromosome with coiled chromonema. Alternate internodes at right angles to each other.
Fig. 21. Early anaphase as the chromosome begins to divide. No separation of chromatids.
Fig. 22. Later stage of first meiotic division showing dual nature of chromonemata and the relations of the chromatids at the chiasma.
Fig. 23. Unequal separation of chromatids.
Fig. 24. Late anaphase with one pair of chromatids in contact while the other pair have separated and contracted.
Fig. 25. A typical daughter chromosome at early telophase showing contraction and coiling of the chromonema.

DESCRIPTION OF PLATE 26

Diagrams illustrating the cytological mechanism of crossing over.
Diagram 1. Pairing of chromosomes at pachytene. The chromosomes are slightly twisted about each other and are separated into their respective chromatids. The maternal chromatids are pictured in black, the paternal chromatids in white.

Diagram 2. Diplotene looping and the formation of nodes and internodes. The exchange of partners between paired chromatids constitutes a chiasma.

Diagram 3. Later diplotene stage as the chromatids become closely paired and form a coiled chromonema. Due to a partial twisting of the chromonemata, about each other or to the coiling of the chromonemata, the chromatids which appear to cross each other at the chiasmas will often be brought in contact with each other.

Diagram 4. Early metaphase. Chiasmas B and C have broken between early diplotene and late diakinesis. Since the close association and coiling of chromatids prevents appreciable movement of chiasmas any stress imposed on the chiasmas, due to unequal contraction of chromonemata, to opening of diplotene loops, or torsion caused by chromonema coiling, will cause breaks in some of the chiasmas. The association of two independent chromatids, one from each parent, into an apparently single chromonema, is indicated by cross lines.

Diagram 5. The four chromatids at late anaphase showing the results of the double crossover. The associated chromatids separate at the second meiotic division.

Diagram 6. Due to coiling of the chromonemata two chromatids may be brought in contact with each other even though the adjacent internodes lie in planes at right angles to each other as shown in this diagram. Gene by gene association in the paired chromatids will cause pairing of the associated chromatids up to the point of exchange of partners, so that breaks in the chromatids are confined to a very small segment of the crossed chromatids, and will result in precise crossover levels between the two chromatids.

Diagrams 7–8. These diagrams show the relations of the chromatids which would result in unequal crossing over. The order of the two alellomorphic genes B and B′ in the duplicated section will depend on the point where crossing over occurs.

Diagrams 9–10. The relations of the three homologous chromosomes at pachytene and at diplotene in triploids. These relations of the chromosomes and chromatids are based on Darlington's description of the chromosomes in triploid Hyacinths and seems to be in accord with genetic results obtained from *Drosophila* triploids.

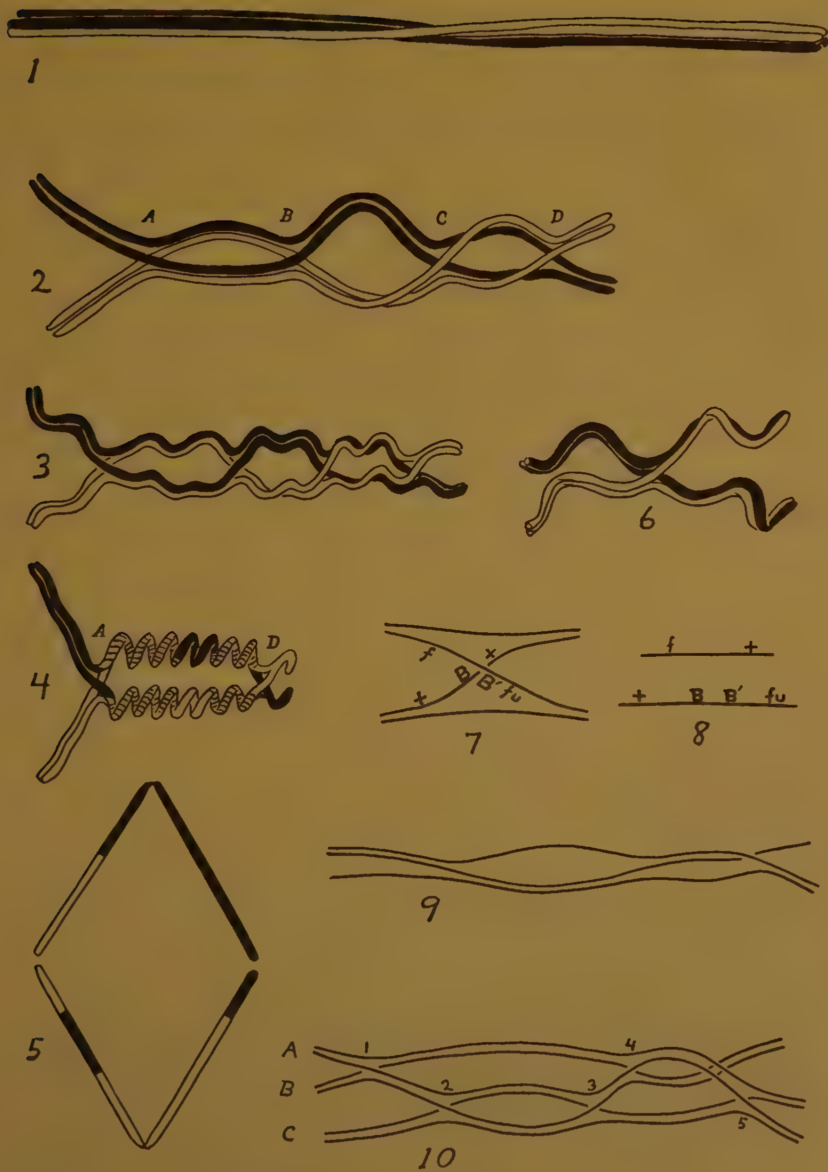
CHROMOSOME NUMBERS IN QUERCUS

Hally Jolivette Sax

The genus *Quercus* is divided into three subgenera, *Cyclobalanopsis Erythrobalanus* and *Lepidobalanus*. These subgenera include more than three hundred species of Oaks. They are found in the temperate regions of the northern hemisphere and in the tropics at high altitudes. They range south to Colombia in America and to the Malay Archipelago in Asia.

There are many hybrids known among the Oaks. Trelease says "So far as my knowledge goes, no hybrids have been detected except between parents of a single subgenus though supposed crosses of the aberrant red oak, *Q. Emoryi*, with the white oaks, *Q. grisea* and *Q. pungens* are reported." Crossing is usually found between very closely related species within the subgenus. Trelease reports fifty-one hybrids in the United States.

The Arnold Arboretum includes among its collections many pure



The Mechanism of Crossing over

species and hybrids of *Quercus*. A number of these were studied to determine the number of chromosomes, the size of pollen grains, and the amount of pollen grain sterility.

The first report on chromosome number in *Quercus* was given by Cosens in 1912. He reported eight chromosomes as the somatic number in *Q. coccinea* Muench.

Wetzel, in 1928, reports eleven as the reduced number for the following species: *Q. coccinea* Wangh., *Q. Dalechampii* Tenore, *Q. glandulifera* Blume, *Q. Koehnei* Ambrozy (*Q. Ilex* × *sessiliflora ?*), *Q. libani* Oliv., *Q. macranthera* Fisch. & Mey., *Q. pontica* K. Koch, *Q. robur* L., *Q. sessiliflora* Salisb. (*Q. sessilis* Ehrh.). The chromosome numbers in the above species were obtained by studying the divisions in the pollen mother cell. The number of somatic chromosomes, determined by studying nuclear divisions in the root-tips, was found to be twenty-two in *Quercus Cerris* L. and *Quercus nigra* L.

In 1929 Grimpu reported the number of chromosomes found in the following species: *Q. suber*, *Q. Ilex*, *Q. coccifera*, *Q. palustris*. He found twelve to be the reduced number. He studied the somatic chromosomes in *Q. cerris* and found twenty-four chromosomes.

Friesner, in 1930, published the chromosome number in ten species of Quercus: *Q. alba*, *Q. macrocarpa*, *Q. Prinus*, *Q. Michauxii*, *Q. Muhlenbergii*, *Q. borealis* var. *maxima*, *Q. velutina*, *Q. coccinea*, *Q. marilandica*, and *Q. prinoides*. He reports twelve as the diploid number of chromosomes in the roots of each of the ten species.

The species of *Quercus* studied in the present work belong to the subgenera *Erythrobalanus* (the Red and Black Oaks) and *Lepidobalanus* (the White Oaks). All the hybrids are from crosses between species of the same subgenus.

The chromosome number was determined from the divisions in the pollen mother cells. Very good figures were obtained from acetocarmine smears. Although the chromosomes were very small, it was possible to get clear figures by this method.

The counts are given in the table included below which gives the species, the place of origin, the number of chromosomes, the average size of the pollen grains and the percentage of sterility found in each species.

In most species the number of chromosomes was very distinctly twelve. In some cases, there were apparent only eleven chromosomes; in others thirteen chromosomes could be counted. As reported by Grimpu, there seems to be some irregularity in the meiotic division due to the loose association of the chromosomes. In all cases the number was 12 or 12 ± 1. The hybrids show the same number. From the table there appears to be a remarkable uniformity in number when the species are of the same or of different subgenera or when they are pure species or hybrids.

Since pollen grain size is usually considered an index to relationship of chromosome number within a genus, measurements of the pollen

grains in the above and additional species were made. Mature pollen grains were mounted in aceto-carmine. They were then measured by means of an ocular micrometer. In order to avoid differences due to swelling on applying aceto-carmine, the spores were measured at the same intervals of time in the different species after fixing. A large number of pollen grains were measured. From these the average size of the grain was computed. The data are given in Table I.

The size of the pollen grains in the different species ranges from 6.8 to 8.7 units with the exception of *Q. dentata*. In this species pollen was taken from two trees, one having pollen grains of 8.7 units in diameter, the other 11.2. It is noteworthy that there is the same range of variation in size of pollen grains in the species where the chromosomes have been counted and have been found to be 12 or 12 $\pm$ 1 as there is where no counts were made, excepting the one unusual case of *Q. dentata*. It would be interesting to determine the chromosome number in both specimens of *Q. dentata* to see if there is any cytological variation connected with the morphological differences.

The amount of pollen grain sterility in the different species was determined by counting the number of poorly developed pollen grains in a field as well as the total number. Several counts were made and the percentages of sterility calculated for each species.

Table I includes the data on sterility. The sterility ranges from three to ten percent with the exception of one of the two trees of *Q. dentata*. This tree, which also had the exceptionally large pollen grains, showed eighty percent sterility. The other specimen of *Q. dentata* had eight percent pollen sterility. This does differ significantly from that of other species. With one exception, there is really no significant difference in sterility between the different species and the hybrids studied. There is a striking uniformity in fertility both in pure species and in hybrids. *Q. ludoviciana*, *Q. Leana*, *Q. exacta*, *Q. Bebbiana*, and *Q. Sargentii*, all hybrids, show no significant difference in sterility from that found in pure species.

The uniformity in chromosome number, in the pollen grain size and pollen grain fertility among both pure species and the hybrids is remarkable. There is a large number of natural hybrids with apparently fertile pollen within the subgenus. Thus in the Oaks we find great variability in morphological characters and a wide geographical distribution with uniformity in chromosome number.

Much of the variability in the morphological characters of *Quercus* is doubtless due to hybridization but it is not associated with any irregularity in chromosome distribution.

DATA ON QUERCUS

Quercus	Chromosome number	Pollen size	Pollen St. %	Habitat
Erythrobalanus				
Q. ludoviciana ×	12 ± 1			N. America
Q. imbricaria	12	7.5	4	N. America
Q. Leana ×	12 ± 1	7.4	8	N. America
Q. exacta ×	12	7.4	7	N. America
Q. ilicifolia		7.9	6	N. America
Q. velutina	12 ± 1	7.0	7	N. America
Q. coccinea		7.7	4	N. America
Q. palustris	12	6.9	6	N. America
Lepidobalanus				
Q. serrata		7.3	6	Asia
Q. Cerris		8.0	3	Asia
Q. macranthera		7.9	6	Eurasia
Q. robur		6.8	10	Europe, N. Africa, West Asia
Q. haas		7.8	7	Asia Minor
Q. alba	12	7.5	3	N. America
Q. Bebbiana ×		7.6	7	N. America
Q. Gambelii		6.9	9	N. America
Q. macrocarpa	12 ± 1	6.9	6	N. America
Q. bicolor	12	7.4	3	N. America
Q. montana	12	7.3	3	N. America
Q. Sargentii ×		7.1	7	
Q. prinoides		6.9	3	N. America
Q. Muhlenbergii	12	6.8	7	N. America
Q. aliena		7.0	4	Asia
Q. glandulifera		7.1	9	Asia
Q. mongolica	12 ± 1			Asia
Q. dentata		11.2	80	Asia
Q. dentata		8.7	8	Asia

Q. ludoviciana = Q. phellos × rubra.
Q. Leana = Q. imbricaria × velutina.
Q. exacta = Q. imbricaria × palustris.
Q. Bebbiana = Q. alba × macrocarpa.
Q. Sargentii = Q. montana × robur.

LITERATURE CITED

Cosens, A. A contribution to the morphology and biology of insect galls. *Trans. Cand. Inst.* **9**: 297–381 (1912).

Friesner, R. C. Chromosome numbers in ten species of Quercus. With some remarks on the contributions of Cytology to Taxonomy. *Butler University Botanical Studies.* Vol. II. paper 7 (Jan. 1930).

Grimpu, V. Sur les chromosomes de quelque Chênes. *Rev. de Bot. Appl. et d'Agric. Colon.* 1929. pp. 176–179.

Rehder, A. Manual of cultivated trees and shrubs. 930 pp. Macmillan and Co. New York, 1927.

Trelease, W. The American Oaks. National Academy of Science xx.

Wetzel, G. Chromosomen studien bei den Fagales. *Bot. Archiv.* **25**: 257–283. 1929.

NOTULAE SYSTEMATICAE AD FLORAM SINENSEM, II[1]

H. H. Hu

Acer Chingii, sp. nov.

Arbor ad 11 m. alta, trunco 60 cm. diam. ,coma ampla patente, cortice calcareo-albido, ramulis glabris. Folia 5-loba, circa 10 cm. diam., basi profunde angusteque cordata, lobis acuminatis integris vel apicem versus sparse adpresseque serratis, lobo medio anguste oblongo marginibus fere parallelis ad 5.5 cm. longo et 2 cm. lato, lobis lateralibus ad 4.5 cm. longis, basalibus ovatis 1–1.2 cm. longis, saepe deorsum curvatis lateribus inferioribus fere contiguis, utrinque reticulata, supra laete viridia et glabra, subtus nervis primariis basin versus satis dense villosis exceptis glabra; petioli ad 3 cm. longi, pubescentes. Corymbi fructiferi circa 5 cm. diam., ut videtur breviter paniculati et multiflori, sed in specimine viso fructus immaturos 4 vel 5 gerentes; flores ignoti; samara alis angulo recto divergentibus nuculo leviter compresso 4 mm. longo incluso ad 18 mm. longis et 7 mm. latis rubro-purpureis extus rectis intus leviter falcatis basin versus angustatis.

Tree to 11 m. high, trunk 60 cm. in diam., with large spreading crown, bark chalky white, branchlets glabrous. Leaves 5-lobed, deeply cordate at base, 10 cm. in diameter, lobes acuminate, entire or sparsely and appressedly serrate toward the apex, midlobe to 5.5 cm. long, 2 cm. broad, lateral lobes to 4.5 cm. long, basal lobes often bending abruptly downward, approximately 10–12 mm. long, reticulate, light green and glabrous above, glabrous except densely pubescent along the midribs beneath; petiole to 3 cm. long, pubescent; corymbs about 5 cm. in diameter, apparently many-flowered, in the specimen at hand with 4 or 5 fruits; flowers unknown; samara with wings spreading at right angle, 1.8 mm. long including the nutlet, wings reddish-purple, straight at back, slightly falcate on the inner side, narrowed at base, to 14 mm. long, 7 mm. broad; nutlet slightly compressed, smooth, 4 mm. long.

KWANGSI: Bin Long, Miu Shan, north of Luchen Hsien, on border of Kweichow, alt. 1220 m., common in woods, *R. C. Ching*, Kwangsi Expedition, Academia Sinica, no. 5980 (type), June 14, 1928.

A species of the section Platanoidea, distinct from other Asiatic species chiefly in the deeply cordate base of the leaf and approximate basal lobes.

Schima bambusifolia, sp. nov.

Arbor ad 15 m. alta, trunco 30 cm. diam.; ramuli glabri. Folia coriacea, elliptica vel elliptico-lanceolata, 5.5–9 cm. longa et 2–2.5 cm. lata, acuta vel longe acuminata, basi cuneata vel fere rotundata, integra vel obscure crispata ad marginem, supra levia, glabra, lucida et intense viridia, subtus glabra et obscure coeruleo-viridia; petioli crassi, 13 mm. longi, glabri. Fructus racemosi, globosi, 1 cm. diam., brunnescentes, albido-punctati; pedicellis crassiusculi, 12 mm. longi; semina reniformia, 5 mm. longa et 4 mm. lata, uno latere leviter conçava, anguste alata.

[1] Continued from p. 48.

Tree to 15 m. high, trunk 30 cm. in diam.; branchlets glabrous. Leaves coriaceous, elliptic to elliptic-lanceolate, acute to long acuminate at apex, cuneate to subrounded at base, entire to obscurely crisped along the margins, smooth, glabrous and dark shining green above, glabrous and dull bluish-green beneath, 5.5–9 cm. long, 2–2.5 cm. broad; petiole thick, 13 mm. long, glabrous. Fruits racemose, globose, 1 cm. in diam., brownish, punctate with whitish dots; pedicels thickish, 12 mm. long; seeds reniform, slightly concave on one side, narowly winged, 5 mm. long, 4 mm. broad.

A species differing from all others in much smaller entire leaves, smaller fruits and seeds.

Kwangsi: Shih wan dar Shan, south of Nanning, alt. 1300 m., common in woods, *R. C. Ching*, no 8020, Oct. 19, 1928 (type), no. 8523, Oct. 27, 1928.

Vatica cordata, sp. nov.

Planta lignosa scandens (fide coll.), ad 4 m. alta; ramuli glabri longitudinaliter striati, lenticellis sparsis elevatis breviter ovalibus instructi, ut inflorescentia luteo-griseo-pubescentes. Folia subcoriacea, oblongo-ovata, 12–14 cm. longa et 7–9.5 cm. lata, basi cordata et 5-nervia, supra glabra et pallide viridia, subtus pallidiora et dense pilis flavo-fuscis sericeo-strigosis; petioli 5–6 cm. longi, glabrescentes. Inflorescentia axillaris, racemosa, folia excedens; alabastra conica, obtusa, 4.5 cm. longa, puberula; bracteolae ovato-lanceolatae, acutae, 1.5 mm. longae; calycis lobi deltoidei, acuti, 1 mm. longi. Fructus calyx tubo brevi sparse puberulo; calycis lobi longiores 2, lineari-oblongi, 7.5 cm. longi et circa 1–2 cm. lati, obtusi vel subacuti, basin versus leviter sensim angustati, minute pilosuli, nervis 3 conspicuis et 2 lateralibus levioribus dimidios lobos tantum percurrentibus; lobi breviores 3, oblongi, 1.5 cm. longi et 4 mm. lati, acuminati et apicum versus dentibus 1 vel 2 instructi; fructus obovoidei, apice rostrati, circa 1.8 cm. longi et 6 mm. diametientes.

Woody climber (fide collector) to 4 m. high, branchlets glabrous, longitudinally striated, with scattered elevated short oval lenticels, branchlets and inflorescence yellowish-gray pubescent, leaves subcoriaceous, oblong-ovate, cordate and 5-veined at base, glabrous and light green above, paler and densely yellowish-brown sericeous-strigose beneath, 12–14 cm. long, 7–9.5 cm. broad, petiole glabrescent, 5–6 cm. long; inflorescence axillary, racemose, longer than leaves; flower buds conical, obtuse, 4.5 mm. long, puberulous; bracteoles ovate-lanceolate, acute, 1.5 mm. long; calyx-teeth deltoid, acute, 1 mm. long; pedicels to 12 mm. long, puberulous; fruiting calyx with short tube sparingly puberulous, large calyx-lobes 2, linear-oblong, obtusish or subacute at apex, slightly narrowed gradually downward, minutely pilosulous, with three strong veins in the middle portion and 2 fainter lateral veins reaching about half of the length of the wings, 7.5 cm. long, about 12 mm. broad, smaller lobes 3, oblong, acuminate and 1- or 2-auricled near the apex, 1.5 cm. long,

4 mm. broad; fruit obovoid, beaked at apex, about 1.8 cm. long, 6 mm. in diameter.

KWANGSI: Bako Shan, west of Poseh Hsien, alt. 900 m. in thicket on cliff, *R. C. Ching*, Kwangsi Expedition, Academia Sinica, no. 7426 (type), Sept. 14, 1928.

A species of the section Synaptea distinct from other species chiefly in the ovate-oblong leaves cordate at base and densely yellowish green sericeous-strigose beneath. That this species is recorded by the collector as a woody climber is exceedingly interesting. If correct, then it may prove to be the first known species of this family to be climbing, and the slightly bending branches certainly look like those of climbers.

This is the second species of the genus *Vatica* discovered in China. The other species, *V. astrotricha* Hance, endemic in Cochin-China but lately discovered in Hainan, also belongs to this section. With the discovery of this species, there are now discovered in China three species of the family Dipterocarpaceae. The third species of this family is *Shorea chinensis* which Merrill discovered in Kwangtung.

Gilibertia angustiloba, sp. nov.

Frutex ad 1.5 m. altus (fide coll.), ramulis glabris. Folia omnia (?) profunde trilobata, ad 16 cm. longa, basi cuneata vel sub-rotundata, glabra, supra laete viridia, subtus pallidiora, lobis lanceolatis, medio ad 15 cm. longo, lateralibus ad 12 longis, omnibus circa 18 mm. latis et apicem versus angustatis acutis, leviter et sparsissime denticulatis denticulis mucronulatis vel integris, nervo medio supra elevato et angusto, subtus minus elevato sed latiore, venulis exilibus, non reticulatis; petioli ad 6.5 cm. longi. Fructus (immaturi) globosi, 4 mm. diam., glabri, calyce obsolete denticulato, disco conspicuo, stylis in columnam 1 cm. longam connatis; pedicelli circa 1 cm. longi.

Shrub to 1.5 m. high (fide collector), branchlets glabrous; leaves all (?) deeply 3-lobed, cuneate to rounded-cuneate at base, to 16 cm. long, glabrous, bright green above, paler beneath, lobes lanceolate, mid-lobe slightly longer than the lateral lobes, all tapering toward the apex, acute, obscurely and very remotely denticulate or entire, teeth mucronate, midrib elevated and narrow above, less elevated but broader beneath, veinlets faint, not reticulate, mid-lobe to 15 cm. long, lateral ones to 12 cm. long, about 18 mm. broad; petiole to 6.5 cm. long; fruit (immature) globose, glabrous, 4 mm. in diameter, crowned with a prominent disk, calyx-teeth obsolete, style connate, 1 mm. long; pedicels about 1 cm. long.

KWANGSI: Shih Wan Dar Shan, south of Nanning, alt. 900 m., under growth in forest, *R. C. Ching*, Kwangsi Expedition, Academia Sinica, no. 8019 (type), Oct. 19, 1928.

A species distinct in its leaves being all (?) deeply 3-lobed with long narrow remotely denticulate lobes which have a prominent midrib and faint veinlets.

Sinojackia Rehderiana, sp. nov.

Frutex ad 5 m. altus; ramuli juveniles stellato-pubescentes. Folia membranacea, subsessilia vel breviter petiolata, obovato-elliptica ad elliptico-oblanceolata vel oblonga ad ovata, ad 9 cm. longa et 4 cm. lata, sed plerumque multo minora (2–3 cm. longa et 1.2–1.5 in ramis florentibus), acuta vel obtusiuscula, basi cuneata vel rotundata vel subcordata, laete viridia, utrinque ad venas et laminae basin versus stellato-pubescentia, ceterum glabra, reticulata; petioli breves, 1–4 mm. longi, stellato-pubescentes. Flores albi, penduli, laxe cymoso-paniculati, pedicellis ad 2 cm. longis et pedunculis gracillimis dense stellato-pilosis, calyx cinereo-stellato-pubescens; 5–6-dentatus dentibus triangularibus acutis 1 mm. longis; corolla profunde 5–6-partita segmentis oblongo-ellipticis, 12 mm. longis et 4 mm. latis, acutiusculis, extus stellato-puberulis; stamina 8 mm. longa, filamentis basi in tubum brevem connatis stellato-puberulis; ovarium 3-loculare, stellato-puberulum, sensim in stylum 6 mm. longum, glabrum, attenuatum, stigmate obsolete 3-lobulato; ovula 8 in quoque loculo, biseriata. Fructus ligneus, indehiscens, apice conico longe rostrato ad 1 cm. longo; pars inferior obovoidens, leviter compressus, in stipitem attenuatus et cum stipite 1.5 cm. longum et 5.5 mm. diam., exocarpio suberosa non fisso, endocarpio ligneo, semen solitarium.

Shrub to 5 m. high; young branchlets stellate-pubescent. Leaves membranaceous, subsessile to short-petioled, obovate-elliptic, elliptic-oblanceolate, oblong to ovate, acuminate, acute or obtusish at apex, cuneate, rounded or slightly cordate at base, serrulate, green and glabrous except sparsely stellate-pubescent along the main veins or at the base of leaves on both surfaces, veins reticulate, to 9 cm. long, 4 cm. broad, usually much smaller (2–3 cm. long, 1.2–1.5 cm. broad at flowering time); petiole short, 1–4 mm. long, stellate-pubescent. Flowers white, pendulous, loosely cymose-paniculate, peduncles and pedicels very slender, densely stellate-pilose, pedicels to 2 cm. long; calyx grayish stellate-pubescent, 5–6-dentate, teeth triangular, acute, 1 mm. long; corolla deeply 5–6-cleft, segments oblong-elliptic, acutish at apex, stellate-puberulous outside, 12 mm. long, 4 mm. broad; stamens 8 mm. long, filaments connate at base into a short tube, stellate-puberulous; ovary lanceolate, stellate-puberulous, 3-celled, style subulate, 6 mm. long, stigma obscurely 3-lobed; ovules 2-seriate in each cell, 4 in each series. Fruit woody, indehiscent, apex conical, long-beaked, to 1 cm. long, lower half of the fruit obovoid, slightly compressed, tapering into a stalk at base, grayish brown, punctate with whitish dots, 15 mm. long with the stalk, 5.5 mm. broad; exocarp corky, not fissured; endocarp woody; seed solitary.

Allied to *S. xylocarpa* Hu, differing in shrubby habit, in thinner leaves, in looser flowers and much more slender and elongated fruits.

Kiangsi: Nanchang, common on low hills, *H. H. Hsiung*, no. 578, in 1929 (fruiting specimen); no. 578b, April 20, 1930 (flowering specimen; type).

I take great pleasure in naming the second species of this interesting genus in honor of Mr. Alfred Rehder, Curator of the Herbarium of the Arnold Arboretum of Harvard University, whose profound knowledge of the ligneous flora of China is unsurpassed by any living botanist.

A SUPPLEMENT TO J. T. P. BYHOUWER, "AN ENUMERATION OF THE ROSES OF YUNNAN."

C. E. KOBUSKI.

IN a former number of the Journal of the Arnold Arboretum[1] Dr. J. T. P. Byhouwer presented a paper dealing with the Roses of the Chinese province Yunnan. This year he planned a second visit to the Arboretum and intended while here to study additional material of Roses from Yunnan recently sent by Professor W. Wright Smith of the Royal Botanic Garden at Edinburgh. We are very grateful to Professor Smith for the loan of this material. Unfortunately Dr. Byhouwer found it inconvenient to visit the United States this year and to make the supplementary study. Since I was actively engaged in the study and writing of the former paper, it was desired that I should complete this study in order that the borrowed material could be determined and returned to the Edinburgh Herbarium without great delay.

The specimens for study were those of a later collection by George Forrest, along with material collected by F. Ducloux, Monbeig, C. Schneider and others.

Sect. SYNSTYLAE DeCandolle, Hort. Monsp. 137 (1813).

Rosa multiflora var. **cathayensis** Rehder & Wilson in Sargent, Pl. Wils. II. 304 (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 85 (1929).

Près de la ville, Yunnan-sen, *F. Ducloux*, no. 637, April 24, 1904.

Rosa multiflora var. **carnea** Thory in Redouté, Roses, II. 67, t. (1821).—Rehder & Wilson in Sargent, Pl. Wils. II. 305, (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 86 (1929).

On the margins of thickets and by streams, Chienchuan-Mekong divide, lat. 26° 30′ N., long. 99° 20′ E., alt. 2440 m., *G. Forrest*, no. 23535, June 1923 (spinous, scandent shrub, 3–6 m.; fls. white to pale rose, fragrant); margins of thickets and by streams, Chienchuan-Mekong divide, lat. 26° 30′ N., long. 99° 20′ E., alt. 2135–2440 m., *G. Forrest*, no. 23573, July 1923 (spinous, clambering shrub, 3–4.5 m.; fls. white, fragrant); margins of thickets and by streams, hills around Wei-Hsi, lat. 27° 12′ N., long. 99° 12′ E., alt. 2135–2740 m., *G. Forrest*, no. 25724, July 1924 (spinous, semi-scandent shrub with arched branches, 2–3 m.: fls. pure white, fragrant).

[1] See vol. x. 84–107 (1929).

The three Forrest specimens cited above present a deviation from typical var. *carnea* in that they all possess white flowers. Also the leaves of no. 25724 are distinctly glabrous while the other two specimens (nos. 23535 and 23573) are densely puberulent on the rhachis, petiole and lower surface of the leaves.

Besides these three cited specimens two other numbers may be mentioned under this variety. These all vary from typical *R. multiflora* var. *carnea* in having smaller, glabrous leaves measuring only 1–2 cm. in length and being distinctly obtuse or rounded at the apex. All together the variation seemed so great that on the first superficial examination one would hardly class them as belonging to the same species. The data of these two specimens are as follows:—Amongst scrub by streams near habitations, Chienchuan-Mekong divide, lat. 26° 20′ N., long. 99° 20′ E., alt. 2440 m., *G. Forrest*, no. 23487, June, 1923 (spinous shrub, 1–3.5 m.; fls. pale yellow); amongst scrub by streams, Chienchuan-Mekong divide, lat. 26° 20′ N., long. 99° 20′ E., alt. 2440 m., *G. Forrest*, no. 23518, July 1923 (spinous, semi-scandent shrub, 3–4.5 m.; fls. fragrant, deep rose). One observes in examining the annotation on the labels of these two specimens that the color variation is very great; the former specimen (no. 23487) with its yellow flowers agreeing with the numbers cited in the paragraphs above while the latter (no. 23518) having rose colored flowers agrees with typical *R. multiflora* var. *carnea* as it is generally known.

Rosa Brunonii Lindley, Ros. Monog. 120, t. 14 (1820).—Rehder & Wilson in Sargent, Pl. Wils. II. 306 (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 306 (1915).

Exact locality and date lacking, northwest Yunnan, *T. Monbeig*, nos. 93 and 94, in 1907.

Rosa Helenae Rehder & Wilson in Sargent, Pl. Wils. II. 310 (1915).—Byhouwer in Jour. Arnold Arb. x. 88 (1929).

Rosa floribunda Rolfe in Gard. Chron. ser. 3, LVIII. 210 (1915), pro parte. —Non Steven, nec Baker.

On trees and scrub in thickets, Chienchuan-Mekong divide, lat. 26° 30′ N., long. 99° 20′ E., alt. 2440–2740 m., *G. Forrest*, no. 23534, June 1923 (scandent, spinous shrub 3–9 m.; fls. white, fragrant).

Rosa longicuspis A. Bertoloni in Mem. Acad. Sci. Bologna, XI. 201, t. 13, (1861); Misc. Bot. XXI. 15, t. 3 (1861).—Rehder & Wilson in Sargent, Pl. Wils. II. 313 (1915).—Byhouwer in Jour. Arnold Arb. x. 88 (1929), where full citation of literature and synonyms is given.

Vallons du Tchong chan, Yunnan-sen, *F. Ducloux*, no. 1210, April 28, 1909; Ko [?]-tsou region de Kiao Kia, *F. Ducloux*, no. 1211, Mai 11, 1909 (plante cueillie par le père S. Ten); Tchen fong chan dans la prefecture de Tchao tong, *F. Ducloux*, no. 635, Mai 11, 1901; open thickets and by streams along ascent of the Li-ti-puie from the Yangtze, lat. 27° 12′ N., alt. 2740–3050 m., *G. Forrest*, no. 13875, June 1917 (spinous shrub, 2–4

m.; fls. fragrant, white, flushed and margined rose); date and exact locality lacking, *E. B. Howell*, nos. 209 and 210.

Rosa glomerata Rehder & Wilson in Sargent, Pl. Wils. II. 309 (1915).—Byhouwer in Jour. Arnold Arb. x. 91 (1929).

Amongst scrub by streams, Chienchuan-Mekong divide, lat. 26° 30′ N., long. 99° 20′ E., alt. 2740 m., *G. Forrest*, no. 23491, July 1923 (spinous, semi-scandent shrub, 3–4.5 m.; fls. fragrant, white).

Sect. BANKSIAE Crépin in Jour. Hort. Soc. XI. 3 (1889).

Rosa Banksiae Ait. f. **lutea** Lindley in Bot. Reg. XIII. t. 1105 (1827).—Byhouwer in Jour. Arnold Arb. x. 92 (1929).

Rosa Banksiae f. *luteiflora* Léveillé, Cat. Pl. Yun-Nan, 234 (1917), nomen.
Rosa Banksiae f. *luteo-plena* Rehder in Bailey, Cycl. Amer. Hort. IV. 1552 (1902).

In thickets and hedges and by streams around villages, Chienchuan-Mekong divide, lat. 26° 30′ N., long. 99° 20′ E., alt. 2440 m., *G. Forrest*, no. 23516, July 1923 (non-spinous? shrub, 2–3 m. with arched branches; fls. bright, soft yellow).

Sect. INDICAE Thory, Prodr. Gen. Rosae, 128 (1820).

Rosa odorata Sweet var. **gigantea** Rehder & Wilson in Sargent, Pl. Wils. II. 338 (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 94 (1929).

Vallons du Tchong chan, Yunnan-sen, *F. Ducloux*, no. 634, April 13, 1904; Eul long Keou region de Kiao Kiá, *F. Ducloux*, no. 1209 April 1909 (Plante cueillie par le père S. Ten); by streams around habitations, Chienchuan-Mekong divide, lat. 26° 20′ N., long. 99° 20′ E., alt. 2440 m., *G. Forrest*, no. 23575, June 1923 (erect shrub 2–3 m. with arched branches; fls. fragrant, rose-pink).

Rosa chinensis Jacquin, Obs. Bot. III. 7, t. 55 (1768).— Rehder & Wilson in Sargent, Pl. Wils. II. 320 (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 96 (1929).

Village dans les vallons au N. E. de la villa, Yunnan-sen, *F. Ducloux*, no. 620, April 11, 1906.

Sect. CINNAMOMEAE De Candolle apud Seringe, Mus. Helv. I. 2 (1818).

Rosa multibracteata Hemsley & Wilson in Kew Bull. Misc. Inform. 1906, p. 156.—Rehder & Wilson in Sargent, Pl. Wils. II. 328 (1915), where full citation of literature and synonyms is given.— Byhouwer in Jour. Arnold Arb. x. 101 (1929).

Without exact locality, Père Monbeig, no. 95, in 1907.

Rosa sertata Rolfe in Bot. Mag. CXXXIX. t. 8473 (1913).—Rehder & Wilson in Sargent, Pl. Wils. II. 327 (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 100 (1929).

Ad vias, regione prope Yung ning, *C. Schneider*, no. 1169, June 19, 1914 (frut. erect. circiter 2 m. alt.)

Sect. SERICEAE Crépin in Jour. des Roses XV. (Nouv. Class Ros. 25) (1891).

Rosa omeiensis Rolfe in Bot. Mag. CXXXVIII. t. 8471 (1912).—Rehder & Wilson in Sargent, Pl. Wils. II. 331 (1915), where full citation of literature and synonyms is given.—Byhouwer in Jour. Arnold Arb. x. 102 (1929).

Djou kou la près Pin tchouan, *F. Ducloux*, no. 627, 1907 (plante cueillie par Jean Ty); without exact locality, *Père Monbeig*, nos. 89 and 90, in 1907.

NOTE ON DARLINGIA SPECTATISSIMA F. V. MUELL. WITH DESCRIPTION OF A NEW VARIETY

C. T. White

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One of the commonest trees in the rain-forests of Northeast Queensland is *Darlingia spectatissima* F. v. Muell. In October 1899 J. F. Bailey named a second species from leaves only as *D. ferruginea*, suggesting at the same time it might when better known prove only to be a more ferrugineous form of *D. spectatissima* F. v. Muell. From flowering specimens recently sent to me by Mr. W. J. Ross and some collected on behalf of the Arnold Arboretum by Mr. S. F. Kajewski I have no hesitation in referring *D. ferruginea* J. F. Bailey as a variety to *D. spectatissima* F. v. Muell. This note is published before a general account of S. F. Kajewski's North Queensland collection as he collected a number of sheets and a distribution of his number as *D. spectatissima* F. v. M. has been made.

Darlingia spectatissima F. v. Mueller, Fragm. Phytogr. Austr. v. 152 (1886).

North Queensland: Rockingham Bay, *J. Dallachy;* Upper Barron River, *J. F. Bailey;* Atherton, *J. F. Bailey, H. W. Mocatta;* Evelyn, *J. F. Bailey;* Yarrabah near Cairns, *N. Michael;* Yungaburra, *J. L. Tardent;* Johnstone River, *T. L. Bancroft, N. Michael.* (See also Domin in Bibl. Bot. XXII (89[1]) 593 [1921]).

Darlingia spectatissima F. v. Muell. var. **ferruginea**, var. nov.

D. ferruginea J. F. Bailey in Queensl. Agric. Jour. v. 402 (1899).

This variety differs from the normal form in young leaves being densely red-ferrugineous tomentose on the lower side, the hairs never totally disappearing even from the older leaves.

North Queensland: Evelyn (local name Brown Oak), *J. F. Bailey* (leaves only), *W. J. Ross* (type of the variety); Atherton, *C. T. White* (leaves only); Malanda, *C. T. White* (leaves only); Gadgarrah Reserve, Atherton Tableland, alt. 800 m., *S. F. Kajewski*, no. 1127.

Common in the rain-forest; medium sized tree up to 25 m.; flowers cream with a delightful perfume.

GRAFT-BLIGHT OF LILAC

KENNETH S. CHESTER

SINCE 1928 I have been engaged in a study of the diseases of Lilacs. Among these there is a destructive and widespread disease of the common Lilac, *Syringa vulgaris*, which is a sequent to a prevailing method of nursery practice and to which I have given the name GRAFT-BLIGHT. It is a disease of exceptional interest and importance and one to which I have given special attention. The investigation of this particular disease has been carried to such a point that I can now give preliminary notice of my findings. A more extended account of this research will be published in the near future.

This disease I have found prevailing in destructive measure in many widely separated places. I have observed it in various nurseries in New England, New York, and New Jersey, as well as in numerous private plantings, while reports have been received of its occurrence in various states as far west as Oregon, in Ontario, Canada, and in Germany.

Plants affected with graft-blight exhibit symptoms of general nutritional deficiency, characterized by a progressive yellowing of the leaf margins and intervenous spaces, reduction in the size and number of the leaves, brittleness and curling of the leaves, premature or abnormally late leaf fall, and the resultant stunting of growth of the plant as a whole. It is limited, for the most part, to plants one to three feet in height and three to seven years of age. Since the symptoms are not usually ameliorated as the plants grow older, the cumulative effects of the disease are shown by those which linger on in a state of depauperate dwarfism; such plants are finally discarded or because of their lowered resistance fall a prey to some secondary disease. A relatively small proportion of blighted plants recovers.

Although the disease gives all appearance of being of abiotic origin, care was taken to demonstrate that it was not of a contagious nature. Attempts were made to transmit it by recognized methods of inoculation such as are used in the case of diseases caused by fungi, bacteria, or viruses. The results of these experiments have proved definitely that the disease is not accompanied by the presence of any pathogenic organism or contagious principle. Likewise the distribution of the disease indicates that it is not of a biotic type.

Although of abiotic origin, the disease shows no consistent relation to the external environment. It occurs under widely varying conditions of temperature and rainfall, on various kinds of soil, and in plants adjacent to absolutely healthy ones.

By a process of elimination the search for the cause was narrowed down to an investigation of the relation of the disease to the grafting method so commonly employed by propagators. It was soon found that the disease characteristically manifests itself solely in Lilacs that were started by grafting or budding on Privet stocks. The trouble was found to lie in this practice of grafting the Lilac onto Privet.

The main burden of proof of this conclusion has rested on a set of grafting experiments repeated during two successive years under controlled conditions with identical results. Scions, all taken from the same Lilac plant, were grafted onto various species of Privet. These were observed in conjunction with control scions from the same source grafted onto Lilac stocks, as well as with cuttings from the same source rooted in the soil. This set of experiments was repeated a second season in a more extensive way. The disease manifested itself in a typical manner in every instance in the Privet-grafted plants, while the controls in all cases remained absolutely free from it. These experiments have been supplemented in other ways, all of which have yielded corroborative evidence.

The results of these investigations have demonstrated unquestionably that the trouble lies in the Privet method of propagation. Incidentally it may be noted that the symptoms vary according to the species of Privet used, but no species of Privet stock tested is satisfactory. In brief it has been demonstrated that an incompatibility exists between Lilac scions and Privet stocks, and that this is expressed by a pathological condition of the Lilac crown. This incompatibility is so pronounced in its severity that large numbers of Lilacs so propagated and sent out by the nurseries for planting fail or languish in the hands of the buyer.

Control of this Lilac blight is obviously to be accomplished by some modification of or by the abandonment of the Privet budding or grafting method and the adoption of some other method of Lilac propagation. Without question budding or grafting on Privet, Ash, *Chionanthus*, *Forsythia*, or other members of the *Oleaceae* is objectionable as usually employed. The Lilac can readily be propagated by the various "own-root" methods of layering, use of suckers, and by hard- and green-wood cuttings. It can also be propagated on Lilac understocks, but this is undesirable because of the suckering of the Lilac stock. Propagation by "own-root" methods has been found to be the most desirable course. It is slower at first, but eliminates all danger of incompatibility, produces a high percentage of successful plants, and is commercially practical.

Pathological Laboratory, Arnold Arboretum,
Harvard University,
September 24, 1930.

NOTES

The Arnold Arboretum during the Fiscal year ended June 30, 1930.

The Arboretum.—The year 1929–30 was unusually dry and very ununfavorable to plant growth in general; little or no rain fell during the months of July, August and September and the winter snowfall was extremely light. Good rains happened in the spring but were insufficient to make good the general shortage; unless heavy rain falls during the summer months the trees and shrubs are likely to suffer. The vicinity of

Boston enjoyed a mild winter, being more fortunate in this respect than many districts in New England, not to mention more distant parts of the country. The frost at no time penetrated deeply into the ground which is fortunate since the snowfall was light. In general, plants in the Arboretum suffered little winter injury, evergreens in particular coming through unscathed. Rhodendrons and other broad leaved plants never wintered better. In January and February some freak weather was experienced, the temperature rising to an abnormal height which was not without its ill effects; on January 8th the thermometer rose to 64° F. and from February 20th to the 25th inclusive a daily average of 65° F. was maintained. This excited the flower buds on a number of plants, especially in those of the Prunus tribe, and subsequent cold weather killed them. The flower buds on the trees of *Prunus yedoensis* and *P. mandshurica* were all blasted; so, too, were the majority on the Siberian Apricot (*P. sibirica*) and related species. The Peach trees in many parts of Massachusetts suffered badly; these early flowering northern trees are readily excited by warm weather in February and the result, as a rule, is disastrous. The advantage of planting them on high ground is well exemplified by trees of *P. yedoensis* on Bussey Hill and on Peters Hill, where the display of blossom was never finer, so the lesson is not to choose low land or supposedly warm corners in which to plant these northern spring flowering trees.

During the autumn the work of extending and spreading out the collections continued; on Hemlock Hill a new group of about one hundred and fifty Hybrid Rhodendrons was made and in the spring a majority flowered. Under the grove of Pines on the right entering South Street Gate a plantation of some five hundred Kalmias was carried out. These two plantations should in the future be among the most attractive features of the Arboretum. The most important gift of plant material the Arboretum received during the year was twelve thousand Narcissi bulbs from Mr. T. A. Havemeyer, of Glen Head, Long Island. These were planted on the land immediately beyond the Administration Building and flowering freely in the spring were a pleasing sight among the grass.

On the whole the plants in the collections flowered well but the drought interfered with the display of fruit and autumn foliage. Among the more interesting plants that blossomed was the new *Stewartia koreana*, an Arboretum introduction from Korea; it promises to be the hardiest and best of its family. For the first time in cultivation blossomed *Platyosprion platycarpum*, a rare Japanese tree related to the American Yellow-wood; this plant was introduced by the Arboretum in 1919 and so far as is known is the only one in cultivation either in this country or in Europe. The Lilacs, now thoroughly rehabilitated, bloomed with great freedom. The collections are beginning to show the good effects of fertilizing, although the application of fertilizers will have to be continued over a period of years to produce any really marked results.

The drought made the fire hazards greater than usual and at times gave cause for much anxiety. The Arboretum proper escaped with one or two minor fires that were put out without any serious damage. On the land adjoining the branch line of the New York, New Haven and Hartford Railway a fire caused either by sparks or live ashes established itself in the peat bog and burned intermittently for more than two months. The railway company behaved very well, paying two hundred and fifty dollars damages. The Park Commission continue to keep the roads in good condition and carry out their part of the contract with Harvard University in an admirable manner. The police protection, however, remains most inadequate, indeed, it may be truthfully said that the Arboretum is unprotected.

During the year 3,222 plants, including grafts and cuttings, were distributed in the United States, Canada, Great Britain, Holland, Germany, Poland and Hawaii and 1,627 packets of seed in the United States, Canada, Great Britain, Ireland, Finland, United Soviet Socialistic Republics, China and New Zealand. There have been received 22,912 plants, including grafts and cuttings and about 15,000 bulbs, from the United States, Canada, Great Britain, Cuba and Japan and 754 packets of seed from the United States, Canada, Cuba, Navassa, Great Britain, Ireland, France, Germany, Poland, United Soviet Socialistic Republics, China, Japan, India, Australia, and New Zealand.

The "Bulletin of Popular Information" was issued as usual and its circulation has enlarged. The regular four numbers of the "Journal of the Arnold Arboretum" were issued; the circulation has increased and it continues to be a valued medium of exchange.

Visitors to the Arboretum were more numerous than in any previous year. Some 1,114 visitors registered at the Administration Building; they came from nearly every state in the union and from several countries of Europe, from South Africa, New Zealand, China, Japan and Java. Among the most distinguished visitors was General J. Smuts, an ardent botanist and one time Prime Minister of South Africa. Another was Mr. Arthur Osborn, who has charge of the arboretum at the Royal Botanic Gardens, Kew, England. Mr. Osborn spent a couple of weeks in the Arboretum and made a list of four hundred plants in cultivation in this Arboretum not growing in Kew Gardens. In July The American Association of Nurserymen held their convention in Boston and some five hundred of them spent a day among the Arboretum collections. Letters seeking information on dendrological and horticultural subjects increased and so, too, did the number of plant specimens sent in for identification. That the Arboretum is doing useful work, is best emphasized by the fact that the response to its annual appeal was more generous than ever before and included several hundred new supporters.—E. H. W.

Pathological Laboratory.—The second year in the history of the Arboretum's research laboratory in Plant Pathology has been marked

by an enlargement of equipment, a growing list of inquiries for help, and an active program of investigation.

Early in the year an experimental greenhouse was erected contiguous to the laboratory. This supplied an imperative need; it has been occupied almost to capacity from the outset with experimental work for which provision elsewhere would have been impossible. A second item of interest has been the inauguration of a pathological herbarium. The private collection of the staff afforded a nucleus as a beginning. To this have been added many hundreds of specimens obtained from the western United States, collected during the summer of 1929 by Mr. G. D. Darker, who was sent out by the Arboretum for that purpose. The object in view is the accumulation of a working and reference collection, as complete as possible, of preserved materials illustrating the many diseases of trees and shrubs. Provision for the care and the housing of such a collection remains to be made.

Inquiries for advice relative to specific diseases of trees, shrubs and forests have been received from about twenty States and Provinces. They have come from nurseries, forest operators, institutions and private owners.

The investigational activities have been varied, and substantial progress has been made on several problems undertaken. A summary follows.

1. A RECONNAISSANCE OF THE FOREST DISEASES OF NOVA SCOTIA. In July, 1929, Nova Scotia was visited at the request of the Provincial Forester, to examine cross sections of its forests from a pathological point of view (J. H. FAULL. Notes on Forest Diseases in Nova Scotia. Jour. Arnold Arb. XI. 55–58. 1930). One immediate outcome has been the starting of an investigation of a disease which has ravished the Beeches there—a disease knowledge of which is of commanding interest because of the imminent threat to this highly valued tree species beyond the limits of that Province.

2. PHACIDIUM BLIGHT OF CONIFERS. The Report of the Arboretum for 1928–29 made reference to the success that had attended our efforts in a study of the cause of this disease and its control in nurseries. Observation and experimentation continued in the nursery of the Brown Company at Oquossoc, Maine, have shown that many species of Conifers other than Spruces are susceptible to Phacidium blight, that the disease is perfectly controllable in all of them, and that without control their culture in areas characterized by certain climatic features is liable to failure. Similar studies have been extended to Phacidium blight in plantations (J. H. FAULL. The Spread and the Control of Phacidium Blight in Spruce Plantations. Jour. Arnold Arb. XI. 136–147. 1930).

3. TRUNK AND ROOT DISEASES OF SPRUCE. A good deal of attention has been devoted during the year to a complex of problems comprised under this designation, and at present they constitute one of our major undertakings.

4. Elm diseases. We have been fortunate to have had with us throughout 1929–30 Dr. C. J. Buisman of the Phytopathologisch Laboratorium "Willie Commelin Scholten," Baarn, Holland. Miss Buisman, who had already made notable researches on the European Elm disease, occupied herself with studies on the diseases of our native Elms, with special attention to those of the American Elm. Towards the end of her sojourn here a finding of great potential importance was made in some diseased Elm specimens sent from Ohio, namely, the presence of an organism that appears to be identical with the causal agent of the feared European Elm disease. As a result the Federal Bureau of Plant Industry was enabled to reach decisions of moment in this connection.

5. Needle Cast Fungi. Studies on this group of fungi have been materially advanced by Mr. G. D. Darker.

6. Lilac diseases. Most important among the diseases of Lilacs is one which is shown to follow a prevalent, but ill-advised practice among propagators. Studies nearing completion, made by Mr. K. S. Chester, have demonstrated the cause and point the way to avoidance of the same. A preliminary account appears in the present issue of this Journal.

7. Various minor topics have been taken up. Mention may be made of one, namely, on a rot of Calla Lily, since the brief paper published on it constitutes one of the the first records of this destructive, imported disease in America, and at the same time has something constructive to offer with respect to its control (K. S. Chester. The Phytophthora Disease of the Calla in America. Jour. Arnold Arb. xi. 169–171. 1930). —J. H. F.

Cytological Laboratory.—The investigation of the chromosome numbers of the species of the more important genera has been continued and several lines of work have been completed. The results obtained throw some light on relationships of different species and in some cases are of considerable interest to the plant breeder.

All of the pure species of *Syringa* were found to have the same chromosome number, but crosses can be made only between species in the same taxonomic groups. The chromosome relationships in certain hybrids indicate that all of the existing species are tetraploids. These results have been published in the Journal of the Arnold Arboretum Vol. xi, 1930.

The chromosome relationships in the genus *Rhodendron* have been found to be most interesting. This polymorphic genus contains nearly 500 species, but representative species of different sections of the genus have the same chromosome numbers or are tetraploids. Hybrids between American and Oriental species show that there is complete compatibility between the parental chromosomes, although the two species may have been separated for millions of years. An account of this work has been published in the American Journal of Botany, Vol. xvii, 1930.

Chromosome counts in *Vitis* show that the species of the subgenus

Euvitis have 19 pairs of chromosomes, while the Muscadinia species has 20 pairs of chromosomes. This difference in chromosome number seems to be associated with fundamental differences in the two subgenera so that no fertile hybrids can be obtained between these two groups. This work has been published in the Proceedings of the American Society for Horticultural Science, 1930.

A cytological study of the *Caprifoliaceae* shows that in most genera the basic chromosome number is the same. There is, however, a great deal of difference in the size of chromosomes of the different genera. No correlation was found between chromosome number or size and the degree of specialization of wood structure. These results were published in the Journal of the Arnold Arboretum Vol. XI, 1930.

The chromosome number and behavior in hybrids between different genera of the Pomoideae of the family Rosaceae have been studied. The fact that the chromosomes of different genera of this group may function together indicates that they are more closely related than the taxonomic classification would imply. Part of this study has been published in the Proceedings of the National Academy of Sciences Vol. 15, 1929. A more complete cytological analysis of the Pomoideae will appear in the next issue of this Journal.

A study of chromosome structure and the nature of chromosome association at the meiotic divisions is of considerable value in the determination of the cause of variations in chromosome numbers in various genera and in species hybrids. A study of chromosome structure in *Secale* and *Lilium* has shown the nature of chromosome association at meiosis and has served as a basis for a cytological interpretation of crossing over. This work appears in the present issue of this Journal.

An investigation of chromosome structure is also being carried on with material which was collected at the Harvard Biological Laboratory, Soledad, Cuba.

Breeding work has been continued, especially with the more important horticultural genera. Seedlings from the crosses made last year are now growing in the new greenhouse.—K. S.

The Herbarium.—The Herbarium now contains 333369 sheets, 18313 having been added during the time from July 1, 1929 to June 30, 1930. Of these accessions approximately 5700 were native of the United States and Canada, 2700 of Central and South America including Mexico and the West Indies, 1615 of Europe and Western and Central Asia, 4800 of China, 1000 of Southern Asia and Malaysia, 400 of Africa, 600 of Australasia and 1000 were cultivated plants. Among the more important collections received during the year the following may be mentioned: from expeditions wholly or partly supported by the Arnold Arboretum were received about 2000 numbers with numerous duplicates collected mostly in the southern and southwestern States by E. J. Palmer, about 850 numbers with many duplicates collected by J. G. Jack in Cuba, about

1000 numbers with many duplicates collected by S. F. Kajewski in the New Hebrides and Santa Cruz Islands, more than 3500 numbers with duplicates collected by W. P. Fang in the Chinese province of Szechuan, nearly 600 numbers with duplicates collected by C. T. White and S. F. Kajewski in North Queensland, about 250 numbers with duplicates collected by J. Mattfeld in Bulgaria. As gifts were received about 360 numbers with duplicates collected by W. Bangham in Central America and the West Indies, and about the same number collected by F. M. Salvoza in Panama and Cuba, about 120 numbers with duplicates collected by Dr. J. Becquaert in Yucatan, and about 540 specimens of cultivated plants from Vilmorin-Andrieux in Paris. By exchange were received from the Sun Yatsen University about 1700 Kwangtung plants, from the Edinburgh Botanic Garden about 500 Yunnan plants collected by G. Forrest, from the Metropolitan Museum at Nanking about 360 plants from Kwangsi collected by R. C. Ching, from the Riks Museum at Stockholm about 330 plants of Tropical America, from the Berlin Botanic Garden about 200 Kamerun plants, from the Yale Forestry School about 350 Liberian plants collected by G. P. Cooper; from the New York Botanic Garden about 1250 plants from E. Asia and the Philippines. Through purchase were acquired about 300 specimens from Argentina collected by Venturi and about 300 specimens from Mexico collected by C. A. Purpus.

Besides the constant use of the herbarium by the staff in the determinations of plants sent in for identification and in the determination of large collections, chiefly from North America and Eastern Asia, the facilities of the herbarium have been used by students of other departments of the University and from abroad as by Mr. Chien P'ei of Chengtu, China, who is working on a revision of the Chinese Verbenaceae and by Mr. F. P. Metcalf of the Canton Christian College who is preparing a flora of Fukien. For study outside of the Arboretum 803 specimens have been sent out on loan to 18 institutions and individuals in this country and Europe.

There have been distributed from the herbarium 17430 specimens to 41 institutions in the United States and Canada and in Europe, Australia and Africa; also 350 wood specimens to two institutions.

To the fruit collection 137 specimens have been added which brings the number of fruit specimens up to 7037. The fluid in which fleshy fruits are preserved has been changed from a formalin solution to an alcohol-formalin solution.

The arrangement and labeling of the wood collection has been finished and the general wood collection now contains 2186 specimens arranged in systematic order, 686 having been added during the year.

Botanical explorations partly or wholly financed by this institution have been carried on in different parts of the world. Dr. H. Humbert who has collected during the second half of 1928 in Madagascar, has spent

the greater part of 1929 in East Africa where he visited chiefly the region of the Great Lakes, Tanganyika, Kivu and Lake Edward, ascended many high mountains, as Kanuzi (3250 m.), Karisimbi (4506 m.), Muhavura and Mikeno (over 4000 m.), Niragongo and Niamlagira (over 3000 m.) and Mt. Runenzori to the foot of the glaciers (4500 m.); he also visited the tropical forests of the upper Congo basin and the Kenya Colony. He returned in the autumn of 1929 to Algiers after having collected more than 5000 numbers with duplicates and he is now working on his collections of which we have received recently the first shipment. Mr. S. F. Kajewski spent the winter 1929–30 collecting in North Queensland and after regaining his health impaired by attacks of fever while in the New Hebrides the preceding summer set out at the end of February for the Solomon Islands and went first to Bougainville Island, the largest island of the group. Professor C. Y. Chiao of the University of Nanking has started at the end of May 1930 for Shantung on a collecting tour for the Arnold Arboretum and Nanking University; he will visit chiefly the central and western part of the province which is yet botanically little known. Professor J. Bornmüller has collected from the end of April to the end of July 1929 in Asia Minor chiefly Anatolia and Paphlagonia. Assistant Professor J. G. Jack has spent again several months, July and August 1929 and January to April 1930 in Cuba continuing the botanical exploration of the region near the Harvard Tropical Garden at Soledad, Cienfuegos. Mr. E. J. Palmer made from the middle of August to the middle of September a collecting trip to southeastern Canada returning through New York and Pennsylvania; he paid particular attention to the species of Crataegus in view of the revision of the American species of the genus in which he is now engaged.—A. R.

The Library.—During the year the Library has added 760 volumes, 252 pamphlets and 1280 photographs, giving a total of 39,195 bound volumes, 9,466 pamphlets and 16,124 photographs. The number of photographs as given covers only the cards upon which they are mounted, sometimes as many as 6 small pictures being placed on one mount, bringing the actual number to nearly 17,000; besides these, 100 photographs taken by Mr. E. J. Palmer in the middle and south western states, 1924–1929, and 144 taken by Mr. Frank N. Meyer in China from 1905 to 1916 have been mounted in albums. In addition to the bound volumes there are over 200 works which were issued in parts, a large number of which are still publishing but many have been discontinued.

Four hundred periodicals are received currently and represent nearly every country, among these there are several new ones from China strengthening our contacts with that part of the world. One hundred and ninety-three come as exchanges for the *Journal of the Arnold Arboretum* and a few for the *Bulletin of Popular Information*.

About 1200 cards have been filed in the catalogue of books and more than 2400 slips for the supplement to the printed catalogue; 1000 cards

were filed in the catalogue of photographs and 4559 in the "Card-index of new genera, species and varieties published by the Gray Herbarium." To the manuscript "Index of illustrations and of new genera, species and varieties of ligneous plants since 1915," prepared at the Arboretum, 3754 cards have been added making the present total 86,851.

Five hundred books have been bound, including periodicals and 1000 titles, and 1280 photographs catalogued.

During the past few years all nursery catalogues offering woody plants for sale have been preserved and they form an interesting and valuable group, representing 152 foreign and 198 American firms with total number of 1750 catalogues and lists.

The rapid growth of the periodical section necessitated more room and 66 new shelves have been added to accommodate it.

Among the more important acessions of the year, some of which have been previously noted in the April issue of this Journal are:—

Walcott, Mary V. North American wild flowers. Vol. 5. 1925. Gift of Mrs. L. A. Frothingham.

Conder, Josiah. Landscape gardening in Japan. 1893.

Schweigger, A. F. Flora Erlangensis. 1811.

Satow, Sir E. M. The voyage of Captain John Saris to Japan, 1613. 1900.

Deering, Charles. Catalogus stirpium, &c.; or, A catalogue of plants naturally growing and commonly cultivated in divers parts of England more especially about Nottingham. 1738.

Chambers, William. A dissertation on Oriental gardening. [With] an explanatory discourse by Tan Chet-qua. 2d ed. 1773.

Maratti, G. F. Plantarum Romuleæ et Sàturniæ in agro romano existentium specificas notas describit inventor. 1772.

Renault, P. A. Flore du departement de l'Orne, ouvrage élémentaire de botanique, composé de la réunion des systèmes de Tournefort, de Linné et de Jussieu. [1804].

Höss, Franz. Monographie der schwarzföhre, Pinus austriaca, in botanischer und forstlicher beziehung. 1831.

Zawadzki, Alexander. Flora der stadt Lemberg. 1836.

Maly, J. K. Enumeratio plantarum phanerogamicarum imperii austriaci universi. 2 teile. 1848.

M'Leod, John. Voyage of His Majesty's ship Alceste to China, Corea, and the island of Lewchew with an account of her shipwreck. 3d ed. 1820.

Gmelin, K. C. Hortus magni ducis Badensis Carlsruhanus. 1811.

Roscoe, William. An address delivered before the Botanic gardens in Liverpool. 1802.

Mott, F. T. Flora odorata. 1843.

Makino, Tomitarô. A manual of the flora of Nippon. 1927.

Stapf, Otto. Index londinensis. Vol. 2, 3. 1930.

WILSON, E. H. Aristocrats of the trees. 1930.

The original drawings by Mr. C. E. Faxon for the revised edition of Professor Sargent's Manual of the Trees of North America have been arranged and suitably bound.

Through the courtesy of its author, Alfred Carl HOTTES, the Library has received "The Gardener's Pronouncing Dictionary," compiled for *Better Homes & Gardens*, 1930.

The names used are principally those in "Standardized Plant Names." The "Manual of Cultivated Trees and Shrubs," by Alfred Rehder, and the "Manual of Cultivated Plants," by L. H. Bailey have been frequently consulted, as has T. S. Lindsay's "Plant Names," and English books which may not be available to American readers.

The botanical names are followed by a clear indication of pronunciation, the common name and a short description of the plant. The list also includes references under the common names and explanations of descriptive terms. Two plates show types of leaves, of flowers, and of fruits.

A book of 88 pages, in paper cover, this little Dictionary meets a long felt need and is bound to prove useful in the questions so perplexing to the student and to the amateur flower lover, the pronunciation of plant names.

From the AMERICAN SOCIETY OF MECHANICAL ENGINEERS, has come their publication "A Bibliography on Woods of the World, exclusive of the Temperate region of North America, and with emphasis on tropical woods," 1928.

It is printed in clear type and consists of 77 pages double column. The entries are numbered from 1 to 1530 and are arranged under the headings General, Tropical America, Europe, Asia and Oceania, Africa. A full subject index ends the volume.

The work was undertaken on the recommendation of the Wood Industries Division of the American Society of Mechanical Engineers in cooperation with the Tropical Plant Research Foundation, Washington, D. C. to investigate the possibilities of applying tropical woods to the wood industries in this country, Professor Samuel J. Record's "Bibliography of the Woods of the World with Emphasis on Tropical Woods" forming the starting point. "The references cover tropical forestry, lumbering, marketing, wood uses, and characteristics, as well as botanical information of an extensive nature on the woods of the world."

Due to our rapidly disappearing forests, the study of the world's forest trees becomes a crying necessity, and a bibliography so complete is a valuable aid in its pursuit.

Mr. F. M. SALVOZA of the School of Forestry, University of the Philippines, has presented to the Library his "Monograph of the Genus Rhizophora, an investigation carried out at the Arnold Arboretum, and submitted as a thesis in partial fulfilment of the requirements for the

degree of Doctor of Science in the Bussey Institution of Harvard University." It comprises 123 type-written sheets and 13 photographic plates and maps.

New serials include:—

FAN memorial institute of biology. Bulletin. Peiping, China. 1929.

FORESTRY. Published by the Japanese forestry association, Tokyo. No. 558. 1929.

FORSTLICHE zeitschrift für das grossherzogthum Baden. Bd. i; ii, heft 1, 2. 1838–42.

BEITRÄGE zur kenntnis des forstwesens in Deutschland. Heft i–iv. 1819-21.

MALAYA—Rubber research institute.
Quarterly journal. 1 → Kuala Lumpur. 1929 →
Bulletin. 1 → Kuala Lumpur. 1929 →

MIYAZAKI. College of agriculture and forestry. Bulletin. 1. Miyazaki. 1929.

NIKITA, Russia. Botanical garden.
Bulletin. 1. Yalta. 1929.
Zapiski. 8. Mockba. 1925.

SINENSIA; contributions from the Metropolitan museum of natural history, National research institute, Nanking. Nanking. Aug. 1929. 1.

MEXICO—Universidad nacional autonoma—Instituto de biologia. Anales. 1. Mexico. 1930.

SUBTROPIKI. Published by Abhâsian scientific society, Agricultural section. No. 1. Suchum, V. R. R. S. 1929.

Among the photographs presented to the Library are over 400 of plants of Arizona taken by Mrs. Susan D. McKelvey in 1929 and 75 by Miss Violet F. Edlmann; 120 views of trees and forests taken in Japan and northern China by Professor J. G. Jack in 1905; 143 photographs, chiefly of flowering and fruiting branches of plants in the Arboretum, taken by Mr. H. A. Gleason, 1927–1929; and 35 of flowers and fruits in the Arboretum by Mr. J. H. Lovell. Mr. E. J. Palmer has added 150 to his photographs of western vegetation and Mr. E. H. Wilson 46 of the Arboretum. The Rochester Park Department has added 95 photographs to its already generous gifts.

The most unique gift of recent years is that of Mr. Frederic A. Delano, consisting of 611 paintings of Chinese fruits, flowers and vegetables by native artists.[1]

In view of the fact that the British Museum Catalogue, Pritzel, Kew Catalogue, and all other sources consulted quote "The Botany of the Voyage of H. M. S. Sulphur, under the command of Captain Sir Edward Belcher, 1836–42, by George Bentham," as 1844, the date on the title-page, it is interesting to note that the copy in the Library of the Arnold

[1] See the April issue, pp. 131–132, of this Journal.

Arboretum is in its original buff paper covers, in which the work was issued in 6 parts, and from which it is evident that the later parts appeared in later years:—

No. 1 comprises pages 1– 16, and plates 1–10. 1844.
No. 2 comprises pages 17– 48, and plates 11–20. 1844.
No. 3 comprises pages 49– 72, and plates 21–30. 1844.
No. 4 comprises pages 73– 96, and plates 31–40. 1844.
No. 5 comprises pages 97–144, and plates 41–50. 1845.
No. 6 comprises pages 145–195, and plates 51–60. 1846.
(index pp. 183–195)

A notice on the cover of part 1 reads:—"On the 1st of January, 1844, will be published Part 1. of 'The Botany of the Voyage of H. M. S. Sulphur.' By George Bentham. As little benefit can accrue to science by the publication of mere catalogues of all the species collected, the descriptive matter will be confined to those hitherto unknown, or to the elucidation of such obscure points, as the specimens assist in clearing up; whilst in selecting the species for illustration, those will be preferred which are more particularly distinguished for the peculiarity of their organization, or with which a fuller acquaintance is desirable in the present state of botanical knowledge. The parts will appear quarterly." —E. D. M. T.

Staff of the Arnold Arboretum, 1930–31

INDEX

Synonyms are printed in *italics*, new names in **bold-face** type.

ERRATA

Page 101 line 1 *for* Raphanastrum *read* Raphanistrum
" 108 line 17 from below *for* Pastanaca *read* Pastinaca
" 137 line 5 *for* intervenes *read* intervene
" 144 line 1 from below *omit* in the
" 154 line 11, from below after (1906) *add* as synon. of *C. hupehensis*